

The Raninidæ: a Study in Carcinology. By GILBERT C. BOURNE, M.A., D.Sc., F.R.S., F.L.S., late Fellow of Merton College, Oxford, and Linacre Professor of Zoology and Comparative Anatomy.

(PLATES 4-7.)

[Read 15th December, 1921.]

MM. A. MILNE EDWARDS and E. L. BOUVIER conclude the Introduction to their Report on the Deomiacea and Oxystomata dredged by the U.S. Coast Survey Steamer 'Blake' with the following sentence:—"Nous avons distrait du groupe des Oxystomes la famille des Raninidés qui nous paraît aberrante à plus d'un titre. Ces Oxystomes anormaux sont représentés par de curieuses formes nouvelles dans les matériaux recueillis par le Blake; nous les étudions avec la plus grand détail, et ils font prochainement l'objet d'une étude très complète." So far as I have been able to ascertain by search in the records of zoological literature, somewhat incomplete as they are through disturbances arising out of the late war, this promised memoir on the Raninidæ has not yet been published, and the following pages give an account of my own studies on this aberrant and, as I shall strive to show, primitive family of crabs. My attention was directed to them some eight years ago, and I spent some time in the attempt to procure a well-preserved specimen of *Ranina*, of which I had several ill-preserved examples collected by Messrs. C. & E. Hose in Celebes. Eventually, after much fruitless correspondence with other naturalists, I obtained a fine specimen of *Ranina dentata* from Professor Kishinoye, of Tokio. It was admirably preserved in spirit, and I have to express my best thanks to him for his trouble in procuring me so excellent an example for study and dissection.

In addition to *Ranina*, I had examples of the following members of the family in the collections of the Oxford University Museum:—

*Notopus dorsipes*, Fabr.; two examples collected by H.M.S. 'Nassau' in the Sulu Sea, 1871-72.

*Raninoides personatus*, White MS., Henderson; one example from the Bay of Bengal, presented to the University by the Calcutta Museum.

*Lyreidus tridentatus*, de Haan; two examples from Port Jackson, presented to the University by the Trustees of the British Museum of Natural History.

Two examples of a species labelled "Notopus," collected in the Sulu Sea by H.M.S. 'Nassau.' These I am describing as a new genus and species under the name of *Notosceles chimmonis*.

I have also been able to examine the following species in the British Museum of Natural History, and take this opportunity of thanking Dr. W. T. Calman for his courtesy and assistance in bringing the material together for examination:—

*Notopoides latus*, Henderson.

*Notopus ovalis*, Henderson.

*Lyreidus Channeri*, Wood-Mason.

*Zanclifer caribensis*, de Freminville.

*Cosmonotus Grayi*, Adams & White.

The above are preserved in spirit. I also had the opportunity of examining a dried specimen labelled *Ranilia muricata*, M. Edw., and am inclined to the opinion that, while it is a distinct species, it is closely allied to and should be placed in the genus *Notopus* of de Haan.

Thus I have had opportunities of studying more or less closely nearly all the known genera and most of the known species of the Raninidæ, which must be accounted one of the most ancient crab families, for it occurs in the Cretaceous along with other forerunners of existing crabs. The proper place of the Raninidæ in classification has always been a subject of dispute. Latreille first placed them among the Brachyura, but subsequently removed them to the Macrura. Milne Edwards in his 'Histoire Naturelle des Crustacés' (25, 1837) includes them along with the Dromididæ, Homolidæ, and Pactolidæ as a tribe of his section Anomura Apterura. De Haan (34, 1850) showed that the resemblances between the Raninidæ and Hippidæ were superficial, and placed the former among the Oxystomata, laying special stress on the affinities of *Lyreidus* to the Leucosiidæ. "Uti in ceteris Oxystomatibus, os Raninoideorum parte anteriore est canaliculatum. Raninoidea et Leucosidea unice sunt formæ inter Decapoda, quorum regiones pterygostomianæ cum sterno cohærent, ita ut maxillarum quintarum articuli primi infra palpos sint dispositi et radices ipsis regionibus pterygostomianis tegantur; unice, quorum cavitates branchiales a parte anteriore simplicem tantum aperturam offerunt, uti jam Cl. Edwards observavit. *Lyreidus* tam distinctum vinculum constituit inter *Raninas* et *Leucosias*, ut vix dubium remanere possit, quin justus hic sit illius familiæ locus."

Boas (4, 1885) retained the Raninidæ among the Brachyura, but laid stress on their abnormal characters, and concluded by saying, "il m'est impossible de comprendre . . . . pourquoi les Ranines sont rangés avec les autres Oxystomes." In the 'Challenger' Reports, Henderson (35, 1888), following Milne Edwards' arrangement, describes the Raninidæ among the Anomura, and the same author, in a subsequent memoir (36, 1893), makes them into a group, Ranidea, equivalent to his groups Dromidea and Hippidea of the Anomura. Ortmann (41, 1892) follows de Haan in placing the Raninidæ in the Oxystomata, and subsequently (42, 1901) erected the

Oxystomata into a division (Abtheilung) equal in value to the Dromiidea (Boas's Dromiacea) and the Brachyura, the last-named division including all other true crabs. This arrangement, with some minor modifications, has been adopted by Alcock (1, 1896), Borrodaile (12, 1904), and Calman (23, 1909). Against these authorities must be set the opinion of A. Milne Edwards and Bouvier, quoted above, and the similar judgment of Boas that the Raninidæ cannot be included in the Oxystomata. But if carcinologists differ as to the exact position that the Raninidæ should occupy among the crabs, it is now generally agreed (except Ortmann [42], who keeps the Oxystomata apart from the Brachyura) that they are true crabs belonging to the section Brachyura and not to the section Anomura of the Decapoda reptantia. Indeed, this was clearly established by de Haan seventy years ago, and it will be convenient to enumerate here the Brachyuran characters of the Raninidæ, most of which were recognised by the clear-sighted author of the volume 'Crustacea' of the 'Fauna Japonica.' They are:—(1) The reduced abdomen and the absence of uropods. (2) The absence of pleopods on the first abdominal somite of the female. (3) The absence of posterior abdominal appendages in the male. (4) The union of the pterygostomial region of the carapace with the epistome. (5) The adherence of the branchiostegite to the thoracic epimera. (6) The reduction of the branchiæ. (7) The absence of an exopoditic scale on the second antenna. (8) The presence of a sella turcica posterior. (9) The expansion of the ischium and merus of the third maxillipeds to form a plate-like covering to the other mouth-parts. (10) The presence of orbits in which the eye-stalks can be concealed, and correlated with this the reduction in size of the first and second antennæ. Other characters might be mentioned, such as the specialisation of the thoracic limbs as organs of locomotion, involving a great development of the apodemes forming the walls of the cavities in which the muscles of the limbs are contained. In other words, it is part of the distinctive facies of a crab that the musculature is highly developed in connection with the locomotory thoracic limbs, and is feeble almost to the point of disappearance in the abdomen. This feature is strongly marked in the Raninidæ.

On the other hand, it is generally recognised that the Raninidæ exhibit a number of Macruran characters which, on the assumption that the Brachyura are descended from the Macrura, are primitive. Among the more important of these are:—The comparatively well-developed rostrum, which, however, is absent in *Cosmonotus*. The proximal segments of the second antenna are not fused with the epistome, a primitive feature also shared by the Dromiacea. The presence of a sternal canal and the relatively well-developed anterior thoracic apodemes. The narrow and keel-like posterior thoracic sternites. The oviducal apertures opening on the coxæ of the third pereopods, another primitive character shared with the Dromiacea. The external lobes of the

second maxillæ are narrow, the inner lobes normal (Ortmann). Finally, as I shall show, the nervous system is more Astacuran in type than in any other Brachyura. In addition, the Raninidæ exhibit a number of features peculiar to themselves, and these I shall discuss in detail in the later part of this paper.

For the present it is only necessary to refer to the theory originally propounded by Huxley and brilliantly sustained by Bouvier in his essay, 'Sur l'origine homarienne des Crabes' (22), that the crabs are not descended from Paguridæ nor from Galatheidæ nor Thalassinidæ, but directly from the Astacura, and in particular from the Homaridæ through the Dromiacea. "Les Dromiacés par l'intermédiaire des Homolodromies ou de formes très voisines, dérivent directement des Homaridés jurassiques ou de Homaridés qui leur ressemblent." Exception being made of such crab-like forms as *Porcellana*, *Lithodes*, and the *Porcellanopagurus* recently described by Borrodaile, Bouvier's theory of the origin of crabs is now generally accepted, and it follows that, if the Raninidæ be true crabs, they must be descended from a Homarid or Nephropsid ancestor by way of the Dromiacea. Thus Bouvier (22) has given convincing arguments for the derivation of the Dorippidæ from the Dromiacea, and Alcock (2) sees in his genus *Cymonomops*, which differs but little from *Cyclodorippe*, a number of Raninoid characters which, he holds, warrant the conclusion that "we have, in fact, in some of these deep-sea forms the clearest evidence of the close relation of the *Ranina* to the *Dorippe* type and quite sufficient justification for accepting de Haan's scheme of the Oxystomata, almost without modification." *Cymonomops*, however, is clearly a highly-specialised Cyclodorippid; it has been placed in this family by Bouvier, and its supposed resemblances to the Raninidæ are of the most superficial character. If the last-named family were descended from the Dromiacea it would hardly be through a Dorippid line, but it is my object to show in the following pages that the Raninidæ, though by definition they must still be included among the crabs, are not derived from a Dromiid ancestor, but have been evolved as an independent group from the Astacura. In sustaining this thesis I shall place reliance first of all on the nervous system, and secondly on the character and degree of development of the endophragmal skeleton.

Our knowledge of the nervous system of the Decapoda is not very extensive, and what we do know is due largely to the researches of Bouvier (21). He has demonstrated that the degree of concentration of the nervous system varies so considerably in the several groups of Decapoda reptantia that it cannot of itself be taken as a sure guide of affinity, but I shall be content to found my argument upon a sentence taken from his essay, 'Sur l'origine homarienne des Crabes.' "Le système nerveux des Crustacés décapodes, en effet, subit une concentration longitudinale régulière à mesure qu'on s'éloigne

des Macroures pour se rapprocher des Brachyures et la réduction qu'il présente dans le sens de la longueur, est un indice, non pas des affinités précises de l'animal, mais du degré d'évolution cancerienne auquel il est arrivé." If we accept this proposition, and for my own part I accept it without reserve, it must follow that a crab with a nervous system of which the ganglia are more concentrated in the longitudinal direction is farther removed from its Macruran ancestry than one in which the ganglia are far less concentrated, and that the former cannot be a progenitor of the latter.

Of the Raninidæ I have been able, thanks to the excellent state of preservation of the example sent me by Prof. Kishinoye, to make a thorough study of the nervous system of *Ranina dentata* and a sufficient study of that of *Lyreidus tridentatus*, of which I possessed two well-preserved examples. I have also dissected the nervous systems of *Notopus dorsipes* and *Notosceles chimmonis*, and was able to ascertain that they are of the same character and the ganglia fully as much extended in the longitudinal line as in *Ranina* and *Lyreidus*, but their state of preservation did not admit of great accuracy in making out details.

Pl. 4, fig. 8 is a drawing of the nerve-ganglion chain of *Ranina dentata*, as seen from above, the whole series being represented as flattened out in one plane. Pl. 4, fig. 9 shows the actual position of the nerve chain as seen from the side, and its relation to the endophragmal skeleton. Owing to the deep infolding of the sternal apodemes of the posterior thoracic somites, the posterior thoracic ganglia and the abdominal ganglia closely applied to them are directed nearly vertically upwards.

The cerebral ganglion is relatively large and quadrangular in outline, and the ocular, antennular, and antennary nerves are of large size; otherwise it does not present any special features. A small pair of nerves passes forward to the rostrum. The circum-œsophageal connectives are long and stout. The small ganglia on either side of the œsophagus give off a fairly stout nerve to dilator muscles of the œsophagus as well as the more slender connectives of the stomatogastric system. The post-œsophageal commissure is well marked. The subœsophageal ganglion mass is large and goblet-shaped in outline, as seen from above, and gives off five stout nerves on either side. These nerves are somewhat swollen at their origins, and the last two come off rather apart from the rest and give the appearance of originating from a separate ganglionic centre. Otherwise the six ganglia supplying the mandibles, first and second maxillæ, and three pairs of maxillipeds are indistinguishably fused in the subœsophageal mass. It will be noticed that the mandibular nerve does not spring from the subœsophageal ganglion but from the circum-œsophageal connectives, some way in advance of the ganglion. The ganglion pair of the chelipeds is distinct, but so closely fused to the subœsophageal mass that the connectives uniting the two are indistinguishable.

The succeeding ganglion pair, supplying the first pereopods, is situated well back in the thorax, and is connected with the pair supplying the chelipeds by two long connectives separated from one another by a well-marked interval. The ganglion-pair of the second pereopods is united with the preceding pair by similarly distinct connectives, but only one-third as long as those connecting the chelipeds and first pair. The connectives between the second and third ganglion-pairs of the pereopods are shorter, but set widely apart, leaving an oval space for the passage of the large sternal artery. The two last thoracic ganglion-pairs, supplying the third and fourth pereopods, are fused together, and the connections between them cannot be distinguished, but the separate ganglia can be clearly recognized. Closely applied to the last thoracic ganglion-pair is the chain of abdominal ganglia, completely withdrawn into the thorax and represented by a short and thick nervous mass divided by distinct transverse constrictions into five segments. The terminal segment apparently represents the fifth and sixth abdominal ganglia fused together. Paired nerves issue from each abdominal ganglionic segment, and pass backwards closely bound up in the same connective-tissue sheath as the fused mass of abdominal ganglia, but they are represented as spread out by dissection in fig. 8. The nerves issuing from the first abdominal ganglion segment can be traced to the first pair of modified copulatory abdominal limbs of the male. In this condensed and abbreviated representative of the abdominal nerve chain no trace of connectives nor of the paired structure of the ganglia can be detected. The abdominal ganglia and the nerves passing from them to the abdomen lie in the concavity of the narrow sella turcica posterior formed by the deeply infolded sternal apodemes of the last two thoracic segments. Pl. 4. fig. 10 is a representation of the ventral nerve chain of *Lyreidus tridentatus*. The general plan is similar to that of *Ranina*, but the details are different. The subœsophageal ganglion is an ovoid mass, formed by the fusion of the ganglia of the mandibles, maxillæ, and maxillipeds. As I could only count five nerves given off from this ganglion on either side, I conclude that the mandibular nerve issues, as in *Ranina*, from the circum-œsophageal connectives, but I was not able to verify this point. The ganglion-pair of the chelipeds instead of being approximated to the œsophageal as in *Ranina*, is placed further back in the thorax and is united with the subœsophageal by a thick cord, in which I could not trace any separation of the connectives in the middle line. My specimen was none too well preserved, but I can say for certain that these connectives are bound together in the same connective-tissue sheath. The ganglion-pairs of the chelipeds and first pereopods are distant and, as in *Ranina*, their connectives are separated by a distinct slit-like space. The posterior thoracic ganglia are more closely approximated than in *Ranina*, and the short connectives between the ganglion-pairs of the first and second pereopods are bound

together in the same connective-tissue sheath posteriorly, leaving only a small circular passage between them anteriorly. The connectives between the next succeeding ganglion-pairs are pretty widely divaricated to admit the passage of the sternal artery, and the last two thoracic ganglion-pairs are so intimately fused that the separate ganglia cannot be distinguished. The abdominal ganglia are precisely like those of *Ranina*, but somewhat larger in proportion to the rest of the ventral chain. In *Notopus dorsipes* and *Notosceles chimmonis* the ventral nervous chain presents much the same characters, but my examples of these species had lain for many years in spirit and were too rotten to admit of exact study. In *Notopus* the ganglion-pair of the chelipeds is separated from the suboesophageal ganglion mass by an interval somewhat shorter than in *Lyreidus*, but the connectives joining them are distinctly paired and are not included in a common connective-tissue sheath.

The above descriptions, with the figures illustrating them, show that the thoraco-abdominal nerve system of the Raninidæ approximates more nearly to the Macruran type than does that of any other Brachyuran—indeed, more nearly than any Anomuran except *Hippa*, in which genus, as I have ascertained by dissection, the thoracic ganglia are spaced fairly evenly along the longitudinal line and are united by distinctly paired connectives, except the last two which are fused together. The abdominal chain also in *Hippa* consists of at least five fairly distant ganglion-pairs united by distinctly paired connectives, but I have not yet finished my observations on this genus, and must postpone the description of its nervous system to another paper.

As compared with the Decapoda, of which the nervous systems have been accurately described and figured, the abdominal ganglia of the Raninidæ most nearly resemble the condition found in *Dromia vulgaris*, as described and figured by Bouvier (22). I have myself verified the accuracy of this description. But in *Dromia* the thoracic ganglia, though distinct, are closely approximated in longitudinal series, and form a sort of oval beaded ring round the perforation for the passage of the sternal artery, as is the case in *Calappa* among the Oxystomes, in *Corystes*, and generally in the Catametopan section of the Brachygnatha. In respect of the longitudinal concentration of the thoracic ganglia, the Raninidæ exhibit a much more primitive condition than *Dromia*. Similarly, the extended thoracic chain of the Raninidæ is in a much more primitive condition than are the approximated though distinct thoracic ganglia of *Galathea* and *Porcellana* among the Anomura, though these are more primitive as regards the abdominal chain. The same may be said in respect of *Eupagurus*, in which the thoracic ganglia are in some respects more completely fused together than in the Galatheidæ. If we carry on the comparison to the Macruran types, the Raninidæ cannot be brought into close relation with the Lobsters, and still

less with the Crayfishes, because in the first-named the thoracic connectives are separate and show but little tendency to lateral fusion. But of all the Macrura they most closely resemble *Nephrops* in this and other respects. In both the subœsophageal ganglion mass is in a very similar state of concentration, the differences being that in *Ranina* the mandibular nerves are given off from the circum-œsophageal connectives (this may be correlated with the great length of these connectives) and in *Nephrops* the ganglion pair of the third maxillipeds retain a certain distinctness. The connectives between the subœsophageal and the ganglion-pair of the chelipeds are very nearly of the same length and in the same condition of incipient lateral fusion in *Nephrops* as in *Notopus*, though the concentration is carried further in the lateral sense in *Lyreidus* and in the longitudinal sense in *Ranina*. The connectives between the ganglion-pairs of the chelipeds and first pereopods are much longer in the Raninidæ than in *Nephrops*, but are equally distinctly paired in both and show no tendency to lateral fusion. The same may be said of the connectives next following. In the Raninidæ the last two thoracic ganglion-pairs are more (*Lyreidus*) or less (*Ranina*) closely fused together. These differences apart, if the long chain of six abdominal ganglion-pairs of *Nephrops* were shortened up to the condition found in the Raninidæ and withdrawn into the thorax, there would be very little difference between the two nervous systems. So far, then, as this part of their anatomy may serve as a guide, the Dromiacea have progressed further from the Macrurous in the direction of the Brachyurous type than have the Raninidæ, but the latter retain many distinct Macrurous features and exhibit specially close affinities with *Nephrops*.

It will be noticed that there is a marked tendency for the thoracic ganglia to form two groups, one at the anterior the other at the posterior end of the thorax, in the Raninidæ. This must be correlated with the powerful development of the first, second, and third pereopods as digging or swimming organs. These limbs are exceedingly strong, and are actuated by largely developed muscles enclosed in remarkably deep cavities formed by the endo-phragmal skeleton. The size and extent of these muscle cavities as compared with those of other Brachyura is one of the most striking features when one undertakes a dissection of any member of the Raninidæ, and the abundant musculature of the limbs makes the dissection of the nervous system difficult. It is also worthy of remark that in *Lyreidus* the last pair of pereopods are very weak and attenuated and the corresponding ganglion-pair is practically unrecognizable, whereas in *Ranina*, in which the last pair of pereopods differs little in size from the rest, its ganglion-pair is distinct and emits large nerves to the limbs.

Two good figures are given in Cuvier's 'Règne Animal,' but otherwise de Haan is the only author who has dealt with the endo-phragmal skeleton of



the Raninidæ. He says (34, p. 136), "thoracis interior structura offert sellam turcicam uti tantum in Brachyuris, atque canalem sternalem uti in Macrouris ceterim tantum invenitur. Apodemata singula tam sterni quam epimerorum ab utraque parte medio thorace junguntur in quoque articulo sternali, canalem sternalem constituenta vertebrarumque formam plane simulantia. Apodemata cephalica pariter adsunt quinque transversa, ita ut *Ranina* hoc respectu oppositæ sunt *Dromiis*, in quibus apodemata thoracica et cephalica separatim versus centrum commune petunt." We have here a combination of Macruran and Brachyuran characters which, when the ancestry of the Raninidæ is in question, deserves close study. As a preliminary to this part of the subject, I must go in some little detail into the structure and morphology of the endophragmal skeleton. It was described both for Macrura and Brachyura by Milne Edwards (25), and since his day does not seem to have been studied in further detail. We have, subsequently, the brief but very accurate description of these structures in the Crayfish by Huxley (38). His figures, however, are not drawn from a point of view that clearly illustrates the structures described, and I shall endeavour, with the aid of new figures, to make clear some points that are necessary for a detailed comparison with the homologous structures in crabs. Fig. 11 is a ventro-lateral view of the sterna and the endophragmal skeleton of the second and third pereopodal segments of the common Crayfish, seen from the left side; the thorax has been tilted over to the right; the outlines of the articular cavities of the limbs have been thickened to make them more conspicuous. Ventrally we see the keel-shaped sternites, and at the outer side of the posterior end of each is a small articular socket, into which fits a corresponding knob on the coxa of the appropriate limb. Above are the corresponding epimera, separated from one another by a groove which is not a suture but a deep infolding of the cuticle, technically known as an apodeme. If we follow this groove down below the upper limits of the articular cavities of the limbs, we see that it bends forwards, then turns rather abruptly backwards, and seems to end just below a little knob which fits into a corresponding cavity on the coxa of the appropriate limb. Thus the articular knobs, which I shall call strophidia, are borne on prolongations of the anterior ends of the pleura, the articular cavities, which I shall call strophingia, on the posterior ends of the sterna\*. The line indicating the epimeral

\* These small articular knobs and cavities have been described in some detail, and their mechanical action has been described by Herrick (37), but though often figured, they seem to have been neglected by other authors. As I shall have occasion to refer to them frequently and to use them as landmarks, I have found it necessary to give them names, and call the socket the *strophidium*, the peg which fits into it the *strophingium*. The names are derived from the peg (*στροφίγγιον*) and socket (*στροφεύς*) hinge of a Greek door. For the correct formation of the diminutive *στροφεύς*, *στροφείδιον*, strophidium, I am indebted to Mr. Eric Barber of Exeter College.

apodeme seems to end just below the articular knob : in reality it is prolonged beyond it, and can be traced along the inner and hinder edge of the twisted lamella or arthropragm that separates each articular cavity from the one next behind it. The arthropragm, in fact, is a double fold of the cuticle or apodeme, continuous with the pleural apodeme ; the two edges of the fold run down rather to the inside of the hinder edge of the arthropragm, and in the entire animal pass respectively into the arthro-dial or joint membrane of the limb in front and the limb behind. At the lower end of the arthropragm the groove forms the apparent boundary between the contiguous sterna, but here again there is no suture ; the sterna are really continuous, and are only separated by apodemes. All this is familiar, but as separate names, epimera, sterna, arthropragms, etc., are given to the various parts, I have thought it desirable, in view of the comparisons that are to follow, to emphasize the fact that these names only apply to local areas and indurations separated from one another by more or less deep infoldings of a continuous cuticle. In the upper and lower parts of the arthropragm its apodeme is shallow, and consequently the arthropragmal partition extends only a little way into the cavity of the body ; but at about the middle of its course the apodeme becomes very deep and gives rise to a lamina running upwards, forwards, and inwards towards the middle line, short of which it expands into horizontally flattened plate with jagged edges, which makes more or less intimate union with its fellow of the opposite side. The laminæ in question are the endosternites : they and their flattened summits form the walls and roof of the so-called sternal canal within which the thoracic nerve-ganglion chain lies. A sternal canal is found in the *Macrura reptantia* and in some *Anomura*, but, with the exception of the *Raninidæ*, it does not occur in the *Brachyura*. Pl. 4. fig. 11 also shows the epimeral apodemes or endopleurites. As the articular cavities slant backwards, the endopleurites alternate in position with the endosternites, and, as is familiarly known, each endopleurite divides internally, sending a posterior branch to unite with the endosternite of the segment behind, an anterior branch to unite with the endosternite in front. The result of all these complicated arrangements is that the cavity of each limb communicates internally with two imperfectly delimited chambers, which may properly be called muscle-cavities as the abductor and adductor muscles of the limbs are attached to the several apodemie ingrowths that constitute their walls. In the *Macrura*, as the articular sockets of the limbs look nearly ventrally and the epimera are not much inclined inwards from the vertical, the muscle-cavities lie in nearly the same horizontal plane and alternate with one another. A consideration of the relative positions of the dorsal strophingia and ventral strophidia by which the coxa of the limb is hinged to the articular frame will show that the outermost and slightly dorsal of the two muscle-cavities encloses the abductor muscles whose action

moves the coxa outwards, backwards, and slightly upwards; the innermost and slightly more ventral muscle-cavity encloses the adductor muscles whose action is the reverse of the abductors.

On comparing the thoracic skeleton of a crab such as *Carcinus menas* with that of a crayfish or a lobster, the differences are considerable. The carapace being removed, the epimera are seen to slope inwards towards the median dorsal line like the roof of a house. The sterna instead of being narrow and keel-like are widely extended laterally, and form by their union the broad ventral plastron across which run a series of transverse grooves indicating the sternal apodemes. As a consequence the sockets of the limbs are placed not ventrally but on the sides of the body, forming a row which is not straight but curved upwards at both ends. In some cases the hinder end of the row curves upwards, the fourth pereopods being dorsal in position. Although *Dromia* is in many respects a primitive crab retaining many Macruran features, its endophragmal skeleton is so characteristically crab-like that it will serve for comparison and contrast with that of the Crayfish. Pl. 4. fig. 12 is a drawing of the left side of the thorax of *Dromia vulgaris* after removal of the carapace. The thorax has been slightly tilted over to the right to bring it as nearly as possible into comparison with Pl. 4. fig. 11, and for simplicity's sake the perspective of the ventral surface of the sternum has been omitted. Fig. 15 (Pl. 5) is a posterior view of the same preparation which illustrates some features not clearly shown in fig. 12.

As in *Astacus*, the strophingia and strophidia, the former situated at the upper ends the latter at the lower ends of the arthrofragms, serve as convenient landmarks. The most conspicuous feature in the crab is the great depth of the arthrofragms, especially those between the muscle-cavities of the segments of the second and third and third and fourth pereopods (intersegments xii/xiii and xiii/xiv). It is also characteristic that the three posterior arthrofragms slope forward, the two anterior arthrofragms backward, in such wise that the flexor muscle-cavities of which they form the walls converge towards a point situated in the middle of the thorax. A third characteristic feature is that, owing to the low pitch of the gabled roof formed by the epimera (see Pl. 5. fig. 15) the abductor muscle-cavities lie above and not, as in the *Macrura*, in the same horizontal plane as the adductor cavities. All these features, which go a long way to make up the characteristic cancrroid facies, are correlated with the habits of crabs. They run much more actively than any *Macrura*, and the attachments for the muscles of their pereopods are proportionally increased. To provide these attachments the intersegmental apodemes are very deep, particularly on the sternal surface and on the sides of the body, and the arthrofragms, instead of being mere flattened bars as in the *Macrura*, are conspicuous partitions extending deep into the body. But their internal

edges stop some way short of the middle line and are not prolonged into conspicuous endosternites. Towards their lower ends they do, indeed, give off triangular or thorn-shaped offsets (such an offset is shown in the intersegmental arthropod  $x/xi$  in Pl. 4. fig. 12), but these are not expanded into flattened summits and do not come into contact with their fellows of the opposite side of the body. Therefore there is no sternal canal. The epimeral apodemes or endopleurites are well-developed in crabs and, as in *Macrura*, they bifurcate at their inner ends, the anterior bifurcation uniting with the intersegmental apodeme in front, the posterior bifurcation with the intersegmental apodeme next behind, as is shown in fig. 12. It should be noted that in all these respects *Dromia* has departed so far from its *Macruran* ancestry and has taken on so completely the characters of crabs, that it has been possible to make use of it as a typical example of this aspect of canceroid structure.

If we now bring the *Raninidæ* into comparison, taking as our example *Ranina dentata*, we find a curious admixture of crab-like and *Macruran* characters, but the latter predominate and the former must be called deceptively crab-like, for a detailed examination shows that they must have originated independently, in relation to the habits of the animal, and not by way of inheritance from any other recognized crabs.

In the first place, as may be seen by a comparison of Pl. 5. figs. 13, 14, and 15, the contour of the thorax of *Ranina* as seen from behind is more like that of a lobster than like that of a crab. In the crab the width of the thorax largely exceeds its height; in the lobster the height clearly exceeds the width; in *Ranina* the height is rather greater than the width. Looking at the sternal surface, *Ranina* has a broad ventral plastron and in so far resembles a crab, but the most cursory inspection shows that it is made up almost entirely of the greatly enlarged and flattened sternum of the tenth segment. The more posterior thoracic sterna, particularly those of the twelfth and thirteenth segments, are narrow and keel-like; indeed, they are proportionately narrower than in the lobster. The broad sternum of the tenth segment is flat and has no vertical depth; that of the eleventh segment has the form of a pair of aliform expansions extending along the posterior edges of the twelfth sternum and making up with it the ventral plastron. Posteriorly these aliform sclerites meet in the middle line to form the short and somewhat thickened body of the eleventh sternum, tilted somewhat upward. The twelfth sternum is very narrow, of considerable vertical depth, and is curved upwards. The thirteenth and fourteenth sterna are still deeper vertically, and are so much tilted upwards that the cavities of the third pair of pereopods look nearly directly backwards and the cavities of the fourth pair look backwards and upwards (Pl. 5. fig. 14). The large articular cavities of the chelipeds are placed laterally, but those of the first

and second pereopods are almost ventral. Thus, in the middle of the thorax, the articular sockets of the limbs have the same position as in the *Astacura*, but at the two ends their position is similar to that seen in crabs (Pl. 5. fig. 17). The epimera of *Ranina* are of great depth and exhibit peculiar features that will be described later; for the moment it is sufficient to note that, owing to the size and depth of the epimera, the arthrophragms are relatively short and as in the *Astacura* are somewhat narrow curved laminæ separating the articular cavities. But, as also in the *Astacura*, the arthrophragmal apodemes are deeply extended into the body for a limited space on either side of the mid-ventral line. These extensions are the so-called endosternites, and in all the *Raninidæ* they are very largely developed, the largest of them, namely the intersegmental pair xi/xii, extending upwards as much as two-thirds of the entire depth of the thorax. As may be seen in Pl. 4. fig. 9 and Pl. 5. fig. 16, the four posterior pairs of endosternites slope sharply forwards from their points of origin from the arthrophragms, but the intersegmental pair ix/x stands nearly vertically and the pair next in front slopes somewhat backwards. The upper ends of the endosternites are widely expanded, and their innermost expansions, the mesophragms of Huxley, unite in the middle line to form the roof of a very well-marked and very deep sternal canal, at the bottom of which lies the ventral nerve-ganglion chain. This is a wholly *Macruran* character and, as we have seen, it is unrepresented in *Dromia*. In this respect, therefore, as in the nervous system, the *Dromiacea* have departed further from the *Astacuran* and have advanced further towards the canceroid type of structure than have the *Raninidæ*. The former cannot be in the direct ancestral line of the latter.

To return to a consideration of the epimeral elements of the thorax. The epimera (fig. 17), with the exception of the last thoracic, have a great extent dorso-ventrally and present features absolutely distinctive of the *Raninidæ*. That of segment ix stands nearly vertical and the broad epimeron of segment x nearly so. These two do not present any specially abnormal features, but the three succeeding epimera slope sharply forwards, so that their upper extremities converge towards the upper posterior angle of the tenth epimeron, and their extensive lateral surfaces are divided into dorsal and ventral moieties by a ridge running obliquely upwards from the hind margin of the articular cavity of the cheliped to the insertion of the abdomen. Against this ridge the lower edge of the branchiostegite fits closely and is held in position by two projections, one near the anterior edge of the eleventh, the other at the posterior edge of the thirteenth epimeron, just in front of the articular cavity of the last pereopods. The lower moieties of the epimera of the eleventh, twelfth, and thirteenth segments are therefore exposed on the surface, and form a somewhat excavated and roughly quadrilateral area between the coxæ of the limbs and the branchiostegite. The

epimeral walls in this area, being exposed, are strongly calcified. This exposure of a large portion of the epimeral surface is a remarkable and unique feature in the Raninidæ. Even in the *Astacura*, where the lower edge of the branchiostegite is free, it reaches down to the bases of the limbs, and in all crabs the lower edge of the branchiostegite is so closely adapted to the coxæ of the thoracic limbs as to leave no passage for water into the branchial chamber behind the chelæ. This peculiarity did not escape the attention of Milne Edwards, but subsequent authors seem to have paid very little attention to it. If we now examine the interior of the thorax, we find that the apodemes between the ventral and exposed parts of the three thoracic epimera in question are shallow and form nothing more than two inconspicuous thickenings internally, strengthening the framework of this part of the flanks but not projecting into the cavity of the body. But the apodemes above the line of the adherence of the branchiostegites are very deep and form well-marked endopleurites which, as usual, bifurcate and their branches unite with the expanded summits of the endosternites next in front and next behind them. It appears that the excessive depth of the sternal canal is correlated with the restriction of the endopleurites to the upper moieties of the epimera or, to put it in another way, with the downgrowth of the ventral edges of the epimera beyond the line of the attachment of the branchiostegite. The ventral extension of the epimera is an adaptive feature, and receives its explanation when the habits of the animals are taken into account. The Raninidæ are digging crabs, with large and powerful chelipeds and first, second, and third pereopods. In many the fourth pair of pereopods is weak and slender, though in *Ranina* this last pair is not much weaker than the others. The powerful digging limbs imply powerful abductor muscles and large adductor muscle-cavities. Reference to fig. 9 shows that these cavities are in fact unusually deep, and their extent is due to the great length of the endosternites within the body and to the large ventral extensions of the epimera forming their outer walls. The same figure shows that, as in crabs, the abductor muscle-cavities lie above and not alongside of the adductor muscle-cavities. But canceroid as this character is, it has clearly a very different origin from the similar arrangement in crabs.

To turn to another feature noted by de Haan, "thoracis interior offert sellam turcicam uti tantum in Brachyuris." What is this sella turcica? The name is due to Audouin and Edwards, and the latter author has described the elements entering into its composition with great minuteness on p. 34 of the first volume of the 'Histoire Naturelle des Crustacés.' Paraphrasing his description, the sella turcica posterior is a little arch or vault, concave from side to side and convex from front to back, formed by the forward extension and fusion together in the middle line of the nearly

horizontally disposed intersegmental apodemes xiv/xv; in other words, the apodemes separating the last thoracic from the first abdominal segment. This sella turcica is not present in all crabs, but where present the arrangements indicated above are due to the presence of a deep longitudinal mid-ventral apodeme in the last one or two thoracic sterna. The effect of this deep folding-in of the terminal thoracic sterna is to raise the hinder end of the last thoracic sternum and to throw its arthropragmal apodemes forward into a horizontal position. The edges of the arthropragms are thus brought into contact, and fuse in the middle line. It will be understood from the above description that the exhibition of a sella turcica is dependent on the formation of a more or less deep apodeme in the mid-ventral line of the penultimate thoracic sternum.

Figs. 13, 14, and 15 are drawings of posterior views of the thorax of the lobster, of *Ranina dentata*, and of *Dromia vulgaris* respectively. In *Homarus*—I should more correctly write *Astacus*!—the penultimate thoracic sternum is large and escutcheon-shaped in posterior view: it has a distinct mid-ventral apodeme and the central area or inescutcheon is membranous. The terminal sternum consists of two distinct quadrangular pieces united at their inner angles, and above these is a curved transverse bar which appears to be a special calcification of the membrane connecting the last thoracic and first abdominal segment. It is not present in *Nephrops norvegicus* nor in the Crayfish (*Potamobius*). On either side of this bar the intersegmental arthropragms xiv/xv diverge outwards to unite by slender ends with the large and peculiarly shaped epimera of the fourteenth segment. From the front edge of the sternum just where it passes into the arthropragm of each side, the two narrow and nearly horizontal episternites run forward diverging from one another; only their tips appear in the drawing. There is no sella turcica. In *Ranina* the penultimate thoracic segment, though relatively smaller than in the lobster, is similarly somewhat escutcheon-shaped. Both it and the ante-penultimate sternum have a deep mid-ventral apodeme, indicated by the median suture in fig. 14 and clearly shown in side view in fig. 9. The last thoracic sternum, clearly recognizable by the position of the two strophidia, is aliform with tapering wings diverging from one another and passing forwards and upwards to unite with the last thoracic epimeron. The arthropragms xiv/xv are triangular plates arising by their bases from the front edges of the V-shaped arms of the last thoracic sternum. Their apices are, in the natural position of the animal, directed forwards and downwards; their inner surfaces are concave and their admedian edges meet and unite in the middle line, thus forming the sides and floor of the deep trough called the sella turcica. Fig. 9 shows the relation of the abdominal nerve ganglia and the nerves given off from them to this trough. The anterior ends of the arthropragms in question diverge from one another and, curving outwards

beyond the intersegmental endopleurites xiii/xiv, unite with the inner edges of the lower part of the endopleurites xii/xiii. The sella turcica of *Ranina* is therefore of large extent, larger than in so typical a crab as *Carcinus maenas*. Among the various Brachyura that I have studied, it most nearly resembles in form and extent that of *Calappa*. But, as mentioned above, the sella turcica is not found in all crabs. Fig. 15 represents a posterior view of the thorax of *Dromia vulgaris*. The sterna of the twelfth, thirteenth, and fourteenth segments can easily be recognised by the strophidia on their outer extremities; the large pair of ventro-lateral projections in front of them belong to the eleventh sternum; their strophidia, being on their anterior face, do not appear in the drawing. The fourteenth (last thoracic) sternum does not differ much in shape from that of *Ranina* and offers resemblances to that of the lobster. The thirteenth and twelfth sterna are irregularly shaped transverse bars, of which the outer portions are calcified and distinctly separated by apodemes, but their admedian portions lose their distinctness and pass into a median membranous pouch, the walls of which are little if at all calcified. There is no trace of a median longitudinal apodeme in this membranous representative of the penultimate and antepenultimate thoracic sterna, consequently there is no sella turcica. The arthrophragms of the intersegment xiv/xv are seen converging forward from the anterior edges of the V-shaped arms of the last thoracic sternum, and in other crabs they unite above with the epimera of their own segment, in front with the arthrophragms of the intersegment in front, but in the absence of the ventral apodeme they fall far short of meeting in the middle line to form a sella turcica. In this respect, then, *Dromia* has progressed less from the Macruran towards the Brachyuran condition than *Ranina*, and this might be fastened upon as an argument in favour of the derivation of the Raninidæ as of all other crabs from a Dromiacean ancestor, but the transversely elongated twelfth and thirteenth sterna of *Dromia* are quite Brachyuran in character and very different from the narrow and keel-shaped corresponding sterna in the Raninidæ.

On the balance the evidence afforded by the structure of the hinder part of the thorax is against the Dromiacean ancestry of the Raninidæ.

Another crab in which the sella turcica is absent is *Philyra lewis*. In view of de Haan's emphatic opinion that the Leucosiidæ are clearly united to the Raninidæ through *Lyreidus*, an opinion which has found favour with subsequent authors, the marked differences in the structure of the thorax demand attention. A detailed comparison of the endophragmal skeletons of the Raninidæ and Leucosiidæ is best reserved for the discussion of the possible derivation of the latter from the former family in another part of the paper, but it may be conveniently pointed out in this place that in *Philyra* the plastron is broadest at its posterior end; the intra-sternal apodemes are nearly



transverse to the long axis of the body (with the exception of xiii/xv and xiv/xv, which are directly obliquely backwards from the middle line), are of no great vertical height, and give off no offset to form a sternal canal. The abductor muscle-cavities are of great length and slope backwards, converging to a point at the postero-external angle of the thorax on either side. There is no mid-ventral longitudinal apodeme and the arthropragm xiv/xv is rudimentary, so there is no trace of a sella turcica. The arrangements of the several parts are as widely different as possible from those in *Lyreidus* or any other of the Raninidæ.

Though de Haan in the quotation given above (p. 33) draws a contrast between the Raninidæ and the Dromiacea in the matter of the "apodemata cephalica," *i.e.* the pleural and sternal apodemes of intersegments v/vi-ix/x, the Raninidæ show more resemblance to the Dromiacea than to the Astacura in this region, and the two first-named groups differ largely from the last. Passing over the obvious differences due to the presence of a broad and flat shield-shaped sternum in the Raninidæ, attention may be directed to the apodemes entering into the composition of the anterior part of the sternal canal. The reader will remember that in the Astacura, of which *Nephrops norvegicus* may be taken as a convenient example, the pleural and sternal apodemes of the three intersegments in front of ix/x, though some are missing and others feebly developed, unite to carry forward the sternal canal towards the region of the mouth. In front of them both the sternal and pleural apodemes, but particularly the latter, of intersegment v/vi are very largely developed, and their expanded internal extremities combine to form a stout platform between the subœsophageal ganglion mass and the stomach, known to the older carcinologists as the sella turcica anterior. Huxley named this platform the cephalic apodeme. In *Notopus* and *Ranina*, the only two genera of the Raninidæ in which I have been able to study these structures in detail, the endosternites and endopleurites of intersegment ix/x are normal (figs. 9, 16, & 17), the former standing nearly vertically above the plastron and ending above in slightly expanded summits which are joined in the usual way by the anterior branches of the corresponding endopleurites. The endosternites of intersegment viii/ix are small and directed backwards to touch the summits of the endosternites behind them. The endopleurite of intersegment viii/ix is minute, is not branched, and converges towards the point where endosternites viii/ix and ix/x come into contact. Intersegment vii/viii shows only rudimentary endosternites, but its endopleurites are fairly well developed, exhibiting a very short anterior branch and a posterior branch which makes connection with endosternite viii/ix. In intersegment vi/vii there is no recognizable endosternite, but the endopleurite is present in the form of a small incurved lamella. Intersegment v/vi is largely membranous, and neither endosternites nor endopleurites can

be distinguished in it. Hence there is nothing to correspond with the sella turcica anterior of the Astacura. In *Dromia vulgaris* much the same elements can be identified as in the Raninidæ, but the sternal and pleural apodemes of intersegment ix/x do not meet to form a sternal canal. Similarly the sternal and pleural apodemes of intersegment viii/ix unite on each side to form a curved shelf running inwards from the thoracic wall, but leave a wide space open in the middle line. The pleural apodemes vi/vii are fairly well developed and project some way inwards and backwards, but are far from approximating in the middle line. The intersegment v/vi is fairly stout, but is simply an arthropragm without any ingrowths that can be distinguished as endosternites, and though the sixth pleura are well developed, they have no inwardly projecting apodemes separating them from the membrane that corresponds with the fifth pleuron. In all these respects *Dromia* has departed further from the Astacuran condition than have the Raninidæ. In another matter also, the Raninidæ stand closer to the Astacura. In the last named, for example in *Nephrops*, the ninth, eighth, and seventh sterna do not lie in the same straight line as the thoracic sterna behind them, but are directed upwards, so that a line drawn through them forms an angle of about  $140^{\circ}$  with a line drawn through the hinder ends of the more posterior thoracic sterna.

In the Raninidæ, as shown in fig. 17 for *Notopus*, a line drawn through the seventh, eighth, and ninth sterna forms an angle of  $134^{\circ}$  with a line drawn through the tenth and eleventh sterna. In *Dromia* the corresponding lines meet at an angle of  $108^{\circ}$ . This is another character in which the Dromiacea have departed further from the Astacuran type than the Raninidæ, but, as regards the six post-oral segments, it would not be quite accurate to say that they have advanced further towards the canceroid type. There are certain points of resemblance between the Dromiacea and the Raninidæ which may be taken as evidence of but slight modification from the common Astacuran stock from which both have descended: not, however, as evidence that one group has descended from the other. The evidence so far tendered shows that the Raninidæ in their nervous system and in the characters of the endophragmal skeleton are much more nearly akin to the Astacura than are Dromiacea; they are, therefore, the more primitive group and cannot have descended from the less primitive. In both groups the departures from the Macruran type as exhibited in the first six post-oral segments are due to the acquisition of a broad sternum in the tenth segment and the upward cant of the sterna immediately in front of it, with which are associated the retreat of the sub-œsophageal ganglion mass into the thorax (see fig. 9 for *Ranina*), the decrease in length of the carapace and the increase in width of its anterior margin. The mouth is also brought to a more anterior and less ventral position than in the Macrura.

Correlated with these modifications is the extent to which the epimera of the post-oral segments are involved in the branchiostegal fold. In most of the Brachyura that I have examined they are more intimately involved than is the case either in the Raninidæ or in the Dromiacea, and the corresponding sterna and arthrophragms are modified and exhibit features departing more widely from the Astacuran type. A preliminary survey leads me to believe that a study of the structure and relations of the first six post-oral segments in the Brachyura will yield results of considerable classificatory value, but any attempt to discuss the subject would involve a long digression, and it cannot be pursued any further in this place.

But, before instituting a comparison between the pre-oral sternites and the adjacent parts of the exoskeleton in the Dromiacea and Raninidæ, it will be necessary to make a considerable digression with the purpose of clearing up doubtful points in the morphology of this region in the Decapoda reptantia, and defining more precisely certain terms which, to say the best of it, are used in an ambiguous sense by carcinologists.

In the Astacura and in Brachyura in general there is in front of the mouth a plate, usually of considerable breadth laterally, but of variable extent antero-posteriorly, to which is given the name of "epistome." Behind this is the triangular, or in Brachyura the more often quadrilateral area known as the "mouth-frame." The confusion arising from the loose application of these names is really remarkable. They are due to Milne Edwards and Audouin, and it will be well to quote the former author *in extenso* (25, vol. i. p. 251): "En arrière des fossettes antennaires, on voit une surface plane, plus ou moins étendue, qui représente le troisième anneau céphalique et qui porte le nom d'*épistome*. L'espace occupé par l'*épistome*, les fossettes antennaires et la base des antennes externes constitue ce que nous appelons la *région antennaire*. . . . Les parties latérales et inférieures de la carapace, que nous appellerons régions ptérygostomiennes, sont toujours dirigées plus ou moins obliquement en dehors et en haut, et sur la ligne médiane elles laissent entre elles un espace vide qui est occupé par l'appareil masticateur et que nous désignerons sous le nom de *cadre buccal*; tantôt ce cadre buccal à la forme d'un quadrilatère assez régulier, tantôt il est triangulaire, et c'est toujours à sa partie antérieure que viennent se terminer les conduits efférens des cavités branchiales." The definition of the "epistome" is sufficiently exact; it represents the sternum of the third cephalic segment, that is, the antennary segment. Huxley (38) calls the epistome "the sternal region which appertains, in part, to the antennæ and, in part, to the mandibles." He was correct in recognising the inclusion of the mandibular sternal element in the "epistome," so we must take the term to connote the conjoined antennary and mandibular sterna. Both Milne Edwards and Huxley further recognised the distinctness of the antennular sternum lying in front

of the "epistome." But the French naturalist, usually so exact in the definition and use of anatomical terms, goes sadly astray in the application of the terms under discussion, and has thus introduced a confusion which has persisted in carcinological literature down to the present day. Thus in vol. ii. p. 170 of the 'Histoire Naturelle des Crustacés' we find it stated of *Dromia*, "l'épistome est triangulaire," but clearly the triangular sternal element here referred to is the *antennulary* sternum (see *infra*, p. 50). In the same place he says, "le cadre buccal est à peu près carré," and it is clear from an examination in this region in *Dromia*, that the "cadre buccal" is the combined antennary and mandibular sternum, that is, by his own definition, the epistome. Again in vol. ii. p. 97 we find it stated of the Oxystomatous crabs, "le cadre buccal est tout-à-fait triangulaire," and on p. 102 of the Calappidæ, "il n'y a point d'épistome distinct." But a study of these crabs shows that the triangular "cadre buccal" is chiefly made up of the antennary sternum, *i.e.*, it is the epistome, which is said to be absent!

Among more recent authors, Calman (23, p. 257) writes: "the antennal sternum is mainly represented by the epistome, a plate of varying shape lying between the labrum and the bases of the antennæ," and further on "the buccal frame . . . . is more or less distinctly delimited by the epistome itself or by a transverse ridge which divides the epistome into two parts, the epistome proper and the endostome or palate." He does not, with Huxley, recognise the inclusion of the mandibular sternum, but there can be no doubt that Calman identifies the greater part of the "epistome" with the antennary sternum. A little further on the same author makes the following statement: "In all the Brachyura the rostrum or frontal plates ends downwards in the middle line a process which unites in front of the ophthalmic and antennular sterna with the epistome and separates from one another the basal segments of the antennules." This represents accurately enough the prevailing opinion on the subject, and indicates quite clearly that the antennulary sternum is not to be regarded as a component part of the "epistome." But, whilst this part of the statement is accurate, the remaining part is most inaccurate, for an examination of a large number of crabs belonging to diverse families shows that, with very few exceptions, the downward process of the front or rostrum does not unite with the antennary sternum, that is with the epistome, but with the antennulary sternum. The fact is so obvious that it is difficult to understand how the error originated, the more so because Milne Edwards, however obscure he may have been on the subject of the epistome, is quite definite and exact on this point. "Le front se prolonge au-dessus de l'anneau qui porte les yeux. Dans le jeune âge, cet anneau reste à découvert antérieurement, et les yeux ne sont pas logés dans des cavités orbitaires complètes; mais, plus tard, la partie inférieure du front se réunit, sur la ligne médiane, à une prolongement de

l'arceau inférieure du second anneau, de façon à entourer complètement le segment oculaire qu'on n'aperçoit plus qu'à l'intérieur de la carapace" (25, vol. i. p. 250).

It is not necessary to push the question further, for the above quotations show that the terms "epistome" and "mouth-frame" (cadre buccal) have no definite connotation, and being incapable of exact application, must be discarded in favour of a more precise terminology founded on an appreciation of the morphological elements entering into the composition of this region. It is, however, no easy task to give such an appreciation.

A consideration of the more simple and primitive arrangements obtaining in the Macrura must precede a discussion of the highly modified relations of homologous parts in the Brachyura, and for this purpose *Nephrops norvegicus* may be selected as an example. Fig. 19 is a frontal and fig. 20 a lateral view of the cephalic segments of this species. In both the rostrum has been cut through near its base, the ocular peduncles have been cut through near their origins, and in fig. 19 the edge of the carapace has been cut away where it overlaps the external boundary of the right antennary fossa. The first point for consideration is, what constitutes the anterior extremity of the cephalothorax? Not, I think, the rostrum. Huxley (38) has given reasons for regarding the rostrum as a forward prolongation of the third or antennary somite, and although, following Milne Edwards, he based his identification on the somewhat doubtful evidence afforded by the anterior head segments of adult Stomatopods, there is no reason to go so far afield to obtain evidence in support of this view. In the deep-sea Penæidæ, *Benthescyrmus altus* and *Hemipeneus spinidorsalis*, the ocular and antennular segments are sufficiently distinct and freely moveable on one another to afford abundant justification for it. It is also evident from an inspection of fig. 20, that in *Nephrops* the ocular segment lies in front of the base of the rostrum and has its proper tergum in the form of a median sclerite of cartilaginous consistency, little if at all calcified, but none the less definite in form and extent and clearly recognizable as a distinct element in the exoskeleton of this region. The side-walls or epimera of the ocular segment are thin and membranous, but the sternum is a distinct triangular piece, scarcely calcified and of much the same cartilaginous consistency as the tergum. It has been recognised by all previous authors. Immediately behind the ocular is the easily recognizable antennular sternum, and to the right and left of it are the articular sockets of the antennules, separated by the arthrophragms ii/iii from the antennary sockets. The antennular segment is completed, as has been shown by previous authors, by the aliform calcified plates which form the greater part of the walls of the shallow excavations in which the ocular peduncles rest when turned outwards and represent the epimera of the antennular segment. I agree with Huxley (38, p. 157) in identifying a

narrow transverse bar at the base of the rostrum with the tergum of the antennular segment. This bar is easily seen from the inside, but does not appear in a front view, being concealed by the base of the rostrum. Right and left of it are two deep crescentic grooves which are the external indication of two deep aliform apodemes to which the anterior gastric muscles are attached. The apodemes in question are known as the procephalic lobes, and various suggestions have been made as to their significance, but, in my opinion, they are simply the well-developed pleural apodemes of the intersegment i/ii. Thus far the interpretations I have given are hardly, if at all, at variance with those of previous authorities, but the homologies of the antennary and mandibular segments present greater difficulties. The so called epistome of *Nephrops*, as also that of the lobster and the crayfish, is clearly made up of two parts: an anterior broad plate the lateral regions of which are produced right and left into broad divergent wings, giving the whole the shape of a broad inverted V. Behind this, fitting closely into the angle of the V, but separated from it by a distinct groove, is a somewhat projecting narrow curved bar the outer extremities of which end in incurved knobs, which knobs are excavated internally to form the strophidia for articulation with the inner articular processes of the mandibles. The presence of these strophidia is of itself evidence that the bar in question is the mandibular sternum. The transverse groove in front of it deepens in the middle line to form a triangular pit or depression and on the inner surface is a corresponding projection—in fact, an apodeme for the attachment of muscles. As transverse apodemes are always intersegmental, this groove with its median apodeme indicates clearly enough the boundary between the antennary and mandibular sterna. The antennary epimeron of either side is represented by the very narrow curved bar forming the outer boundary of the antennary socket. This bar is united by a membranous fold to and is overlapped by the fold of the anterior margin of the carapace forming the commencement of the branchiostegite. Posteriorly this bar bends inwards to form the thickened interned rim of the antero-lateral margin of the antennary sternum, and though it is completely fused with the latter, I do not doubt that this thickened rim represents the intersegmental arthropod iiii/iv. Externally the antennary epimeron expands and passes, without any obvious line of demarcation, into the calcified plate marked *x* in fig. 18. In *Nephrops* this plate is firmly fused to the outer edge of the V-shaped antennary sternum, and is set back at an angle to it in such wise as to form the inner and upper wall of the anterior part of the exhalant branchial canal, but in both the lobster and the crayfish it lies more nearly in the same plane as the antennary sternum and takes little or no part in the formation of the branchial canal. The postero-internal margin of this plate is thickened, produced backwards, and engages in a groove on the front surface of the

mandible, thus forming the hinge-line about which the mandible rotates. The postero-external edge of the plate is ill-defined and passes into an imperfectly calcified area forming the roof of the branchial canal. The membrane narrows posteriorly, and arriving at the external articular process of the mandible, again becomes calcified and thickened to form a rather large strophidium for articulation with the mandible. After comparison with many other species, I have satisfied myself that the whole of this area, calcified in front and behind, but imperfectly calcified or membranous in the middle, represents the epimeron of the mandibular segment, which in the *Astacura* is fused to the antennary epimeron, but in some primitive *Brachyura*, as I shall show subsequently, is quite independent of it and also of the antennary sternum. Relying on these interpretations which, I venture to think, will be accepted by anyone who makes a careful comparative study of this region, I shall henceforth discard the misleading and purely topographical names in general use and speak of the sterna, epimera, etc., of the various segments.

Before bringing the *Raninidæ* into comparison it will be well to consider the characters presented by some other *Oxystome* crabs, particularly of the *Dorippidæ* from which, according to some authors, the *Raninidæ* are descended. I have studied *Dorippe lunata*, M. Edw., *Æthusa ciliatifrons*, Fax., and *Æthusina gracilipes*, Thiers. Of these the last-named species shows the most primitive and interesting features, and its mouth-frame and antennary region are depicted in fig. 21. The basal joints of the antennules are enormously inflated and interposed between the exposed portions of the ocular peduncles and the rostrum. The antennæ have a four-jointed peduncle and a fairly long flagellum; the basal joint is small but freely moveable. The downward process of the front or rostrum articulates with the antennular sternum, the latter being produced right and left into wings which are adapted to the shape of the inflated basal joints of the antennules. In this species the antennular sternum is largely exposed, only its posterior margin is overlapped by the front end of the spout-shaped antennary sternum. The latter sclerite is well defined and the sutures uniting it to adjacent parts can be seen clearly. It consists of a central somewhat scutiform plate with antero-external projections of which the edges are inrolled ventrally to form the spout-shaped *Oxystomatous* mouth. It is to the hinder ends of these lateral infolded projections that the pterygostomial processes of the carapace are united. Behind the body of the antennary sternum is the mandibular sternum, a very slender but distinct and calcified curved bar. Right and left, intervening between the lateral wings of the antennary sternum and the outer ends of the mandibular sternum, are two distinctly defined oval plates forming the roof of the anterior part of the branchial canal and extending so far backward that they supply the articular strophingia for

the external articular processes of the mandibles. There can be little doubt that these are the epimera of the mandibular segment, and that they are homologous with the less sharply defined areas similarly identified in the *Astacura*.

In *Æthusa ciliatifrons* the arrangements are very similar to those in *Æthusina*, but the individual sclerites are not so easily distinguished. In this species the spout-shaped anterior end of the antennary sternum is produced so far forwards that very little of the antennular sternum can be seen in a surface view. The mandibles also are reduced in size and the mandibular sternum is membranous. In *Dorippe lanata* the spout-like anterior end of the antennary sternum is produced forward to such an extent that it articulates with and overlaps the downward process of the rostrum, thus completely concealing the antennular sternum. This is one of the rare instances in which union is effected between the rostral process and the antennary sternum. In *Dorippe* as in *Æthusa* the mandibular sternum is almost wholly membranous, exhibiting only two small calcifications in the region of the strophidia. The mandibular epimera are large and distinct, triangular in shape, the apices of the triangle produced backwards. The body of the antennary sternum exhibits a large central boss in front of the mandibular sternum, which might, at first sight, be taken for a forward median extension of the latter, but it obviously has no connection with it.

After this survey of one of the families of the Oxystomatous crabs, the Raninidæ may be brought into comparison. Fig. 22 is a front view of the present region of *Notopus dorsipes*, all the appendages being removed with the exception of the right mandible and the left ocular peduncle. Fig. 23 is a similar view of *Ranina dentata*, and figs. 24 and 25 illustrate the same regions in *Notosceles* and *Lyreidus*. For descriptive purposes *Notopus*, a less modified genus than *Ranina* or *Lyreidus*, will be taken as the example of the family. The first thing to be observed is that the antennary sockets are relatively large and situated behind rather than to the sides of the antennular sockets. In this respect *Notopus* more nearly resembles *Homarus* than *Nephrops*, for in the latter the antennary sockets are displaced laterally. Reference to fig. 29 shows that in *Notopus*, as in all Raninidæ, the antennary peduncle is five-jointed, the basal joint being freely moveable, short antero-posteriorly but of relatively considerable width ventrally, and it bears the excretory aperture on a distinct prominent tubercle.

In *Notopus* and in *Ranilia*, M. Edw., the antennary flagellum is multi-articulate and of considerable length, with special features which will be referred to later. All these characters are Macruran. The antennules (fig. 28) with their enlarged basal segments and abbreviated few-jointed external and internal flagella are more canceroid in character, but the basal joints are not inflated to anything like the same extent as in the Dorippidæ



and the antennary sockets lie well behind the ocular peduncles; there are no antennular fossæ internal to the orbits. The ocular peduncle of *Ranina*, as is well known, exhibits these calcified segments bent at an angle to one another when the peduncle is retracted into its orbit. Reference to fig. 22 shows that there are similarly three segments in the ocular peduncle of *Notopus*, but the two proximal are very short, the greater part of the peduncle being formed by the elongated distal segments which, when turned backwards and downwards, rests in an elongated orbital excavation fringed with hairs. There is no division of the orbit by a downward growth of the front external to the antennules, and the proximal segments of the ocular peduncles are inserted close to the middle line on either side of the rostral downgrowth. In all these respects the Raninidæ have departed very little from the Astacuran type and differ from the more canceroid characters exhibited by the Dorippidæ. In *Notopus* the downward process of the rostrum is narrow and strongly keeled ventrally; its dovetail-like articulation with the antennular sternum is well seen in fig. 22. The antennular sternum is escutcheon-shaped, strongly keeled in the middle line, and narrow posteriorly. It has a certain amount of mobility on the antennary sternum, which latter structure is a broad triangular or rather V-shaped plate the apex pointing forward, the antero-lateral margins raised and thickened but not infolded and forming part of the inner wall of the antennary sockets: more posteriorly these margins are united to the pterygostomial lobes of the carapace. The ventral surface of the antennary sternum is deeply excavated to form the exhalant orifice of the branchial canals; its anterior moiety is divided into right and left channels by a low median ridge, posterior to which the right and left branchial canals are separated from one another by a large ventrally projecting hood. This hood, which is characteristic of the Raninidæ, is the greatly developed median part of the mandibular sternum, and its postero-external corners are produced right and left into curved horns at the extremities of which are the strophidia for the articulation of the mandibles. The suture between the antennary and mandibular sternum is well marked in all the Raninidæ I have examined. The shape and size of this hood-like mandibular sternum and its relations to the antennary sternum in front and the labrum behind are shown for *Ranina* in the perspective sketch (fig. 26). The figure also shows the curved lines of hairs guarding the exit of the branchial canal; the posterior and more prominent line of hairs marks off an oblong plate forming part of the roof of the branchial canal, and as a distinct suture can be observed internally corresponding to the external line of hairs, I identify this oblong plate with the mandibular epimeron. In *Notopus* the exit of the branchial canal is guarded by a diffuse hairy patch, and the area behind this, drawn out into the triangular projection shown in fig. 22, must be taken to represent the mandibular epimeron,

but it is so intimately fused to the antennary sternum that no suture is visible.

Posteriorly the mandibular epimeron is continued into the flexible membrane forming the roof and outer wall of the branchial canal. In *Notosceles* (fig. 24) the antennary sternum is very short, is easily separable from the antennular sternum, and the intersegmental arthophragm iii/iv in front, and the mandibular epimera appear to be wholly membranous. In *Lyreidus*, on the other hand (fig. 25), in keeping with the great elongation of the pre-oral region of the carapace, the anterior part of the antennary sternum is greatly produced and to a certain extent overlaps, but does not conceal, the antennular sternum. The regions of the mandibular epimera are also produced far backwards on either side of the mandibular sternum and are calcified, but I cannot find any line of division between them and the antennary sternum. It should be observed that in *Lyreidus* the pterygostomial lobes of the carapace are produced far in front of the mandibles and are united for a considerable distance with the edges of the antennary sternum, a condition very different from that in the Leucosiidæ, with which *Lyreidus* has so often been compared.

From what precedes it is evident that the Raninidæ diverge so much from the Dorippidæ and are so much more primitive in several important particulars, that they cannot be descended from the latter family. Nor does a comparison of the pre-oral segments give any support to the descent of the Raninidæ from the Dromiacea. Fig. 27 is a frontal view of the antennary and oral regions of *Dromia vulgaris*. The antennæ and antennules have been removed and also the left ocular peduncle, but that of the right side is left in place. The whole facies is more cancrioid than in the Raninidæ. The proximal ends of the ocular peduncles, concealed behind the inflated basal joints of the antennules when the latter are in place, are membranous. The antennular and antennary fossæ are small and lie in nearly the same transverse line. The orbits so far resemble those of the Raninidæ that there are no downward processes of the front external to the antennules. The median triangular shield with the apex directed forward is the antennular sternum, and evidently is what Milne Edwards called the "epistome" (*loc. cit.*). It is separated by a distinct but shallow membranous apodeme from the antennary sternum behind, and there is a certain amount of mobility between these sterna. The apex of the antennular sternum fits into a deep depression of the downward process of the rostrum, but can easily be pulled out of it. The antennary sternum forms the anterior boundary of the so-called mouth-frame, and consists of a median bilobed area and two lateral wing-shaped areas marked off from the former by grooves. The two lobes of the median area are nearly square in outline and separated from one another by a deep median fissure: their anterior margins are thickened and truncated, forming a prominent ledge behind the base of the antennular sternum.

Each of the lateral wings is armed anteriorly with a prominent spine; its outer border is nearly straight and makes nearly a right angle with the transverse ledge formed by the median lobes; its inner border is thickened and curves round the outer extremity of the mandibular sternum. The last-named structure is a projecting curved bar intimately fused to the median area of the antennary sternum, but marked off by a groove which in the middle line deepens to form a triangular fossa. Laterally the mandibular sternum seems to terminate in a pair of incurved prominences for articulation with the inner articular processes of the mandibles, but is clearly prolonged beyond these as a pair of diverging horns intimately fused to the postero-internal edges of the aliform external areas of the antennary sternum but projecting slightly beyond the latter. The mandibular epimera are largely membranous, but their antero-internal ends are calcified to form the two plates marked in fig. 26 which form the roof of the anterior part of the exhalant branchial canals. A comparison of figs. 19, 22, and 27 will, I think, convince the reader that in the whole make-up of the pre-oral region the Dromiacea have departed further from the Astacuran type than have the Raninidæ, particularly in the reduction of the rostrum, the greater development of the suborbital lobe of the carapace, the membranous condition of the inner moieties of the ocular peduncles, the size and relative positions of the antennular and antennary fossæ. Further, the modifications of the antennary and mandibular sterna are widely divergent in the two groups. It may be objected, and there would be some force in the objection, that the genus *Dromia*, on which I have relied for study of details, is a much modified and specialised genus of the Dromiacea, and that I should have directed my attention rather to the more primitive genera, *Homolodromia* and *Dicranodromia*, on which Bouvier so largely relies in establishing his theory of the Astacuran origin of crabs. Unfortunately examples of these rare and instructive forms were not at my disposal, but they have been described in sufficient detail by A. Milne Edwards and Bouvier (28), and a reference to pl. i. fig. 2 and pl. iii. fig. 2 of their admirable memoir will convince the reader that I am justified in extending the results of my study of the genus *Dromia* to the more primitive members of the group and in asserting that in the make-up of the pre-oral region, as in other characters previously dealt with, the Dromiacea have departed more widely from the Astacuran type than have the Raninidæ, and therefore cannot be enrolled in the ancestry of the latter.

I submit that, by a detailed study and comparison of the nervous system, the endophragmal system of the thorax, and the cephalic segments, I have proved the first part of my thesis and have shown that, whilst there is plenty of evidence for deriving each group separately from an Astacuran ancestor, the Raninidæ cannot be directly descended from a Dromiacean stock. The

palæontological evidence available, as far as it goes, supports this thesis. The Raninidæ are ancient forms among crabs, and when they make their first appearance have their characteristics fully developed. The earliest fossils of which I can find a sufficiently exact account are *Raninella Trigeri* from the grès verts of Maine (France) and *R. elongata* from the cretaceous beds of the Sarthe. Both deposits belong to the Turonian division of the Cretaceous. In these early Raninidæ the carapace is of elongated oval shape, broadest in the anterior third; the "buccal frame" is so much elongated that it is nearly half the length of the body; the thoracic sterna, wide between the first pair of legs, become narrowed between the second pair and are reduced to linear dimensions between the posterior pairs of pereopods; the four pairs of pereopods are compressed and adapted for digging in sand (A. Milne Edwards 27). This is the description of a very typical Raninid of fossorial habit showing no greater affinity to the Prosoptonidæ or to *Protocarcinus* (*Palæinachus*, Woodw.) than do existing members of the group. The presence of *Ranina marestiana* and *Notopus Beyrichii* in the Eocene show that modern genera of the Raninidæ were then differentiated and well established. Bittner's (3) excellent figure of the latter species might pass for a representation of the anterior half of the carapace of a modern *Notopus*. Perhaps the geological evidence proves no more than the antiquity of the Raninidæ, but that antiquity affords support to the argument that they had an independent origin from the Astacura.

If, then, they are not descended from a Protocarcinid-Prosoptonid stock by way of the Dromiacea, *a fortiori* the Raninidæ cannot be descended from the Dorippidæ or Cyclodorippidæ, which are themselves derived from the Dromiacea. From what has preceded it is evident that they cannot be; their primitive nervous system and endophragmal skeleton is sufficient evidence of that. On the same reasoning, the Dorippidæ cannot be descended from the Raninidæ, for it has been shown that their ancestry is altogether different. So one of the families, and that the most primitive, of the remainder of the Oxystomata is excluded from relationship with the Raninidæ. What, then, of the two remaining Oxystome families, the Calappidæ and the Leucosiidæ. They are classified with the Raninidæ because the majority of carcinologists have found it difficult to believe that the Oxystome "mouth frame" could have been acquired independently by different lines of descent. But since the Dorippidæ are excluded from relationship with the Raninidæ this objection no longer has any force. But there is room for the opinion that the Calappidæ and Leucosiidæ are descended from the Raninidæ, and I have already quoted (p. 26) de Haan's positive opinion that *Lyreidus* is an annectant form with the Leucosiidæ. There are, of course, many points of difference between the Raninidæ and the two above-named families. It would be an easy though a lengthy task

to enumerate them, but the labour may be spared because the majority of them could plausibly be explained on a theory of descent with modification from a Raninid ancestor. This explanation could be given satisfactorily in such matters as the concentration of the nervous system, the disappearance of the sternal canal, the broadening of the posterior thoracic sterna, and a large number of other characters. But it cannot apply in the case of structural features which have been profoundly altered or have disappeared altogether in the Raninidæ but are present and exhibit normal relations in Calappidæ and Leucosiidæ.

To take first a feature peculiar to the Raninidæ, the marked reduction in vertical depth of the posterior part of the branchiostegite whereby a considerable area of the epimera of the eleventh, twelfth, and thirteenth segments is left uncovered. This is by no means primitive but a definite specialisation, and I have attributed it to the burrowing habits of the family. The Calappinæ are certainly and the Matutinæ largely sand-burrowing crabs, but in both the lower edges of the branchiostegite fit very closely to the coxæ of the pereopods. In the Leucosiidæ, which are supposed to resemble the Raninidæ more closely than other Oxystomes, the adaptation of the lower edges of the branchiostegite to the coxæ of the pereopods is particularly close and elaborate. It cannot be argued that the original and more primitive relations of the branchiostegite to the epimera were re-established when the necessity for enlarged muscle-cavities for the pereopods disappeared with the assumption of new habits by the Calappidæ and Leucosiidæ, for the muscle-cavities are very large in these families but their enlargement is provided for in a very different manner. In the Leucosiidæ the arrangement of the elongated abductor muscle-cavities is peculiar and interesting, but there is no room to describe it in this place.

In all the Raninidæ the posterior margin of the pterygostomial region of the carapace is closely united to a broad offset of the tenth sternum in front of the cheliped. Consequently there is no inhalant branchial orifice in front of the cheliped, and the epipodite of the third maxilliped is aborted, though a trace of it remains in the form of a vestigial setobranch. In the Calappinæ and Matutinæ the pre-chelipedal inhalant aperture is conspicuous and the epipodite of the third maxilliped well developed. It cannot seriously be maintained that these structures have been re-acquired in these two sand-burrowing sub-families. In the Leucosiidæ, however, the posterior margin of the pterygostome is as intimately fused with the plastron as in the Raninidæ, and with the disappearance of the pre-chelipedal branchial orifice the epipodite of the third maxilliped has disappeared even more completely than in the Raninidæ, for there is not even a vestigial setobranch. A similar state of things occurs in some of the Cyclodorippidæ, but need not be discussed here because the Dorippidæ have already been excluded from

relationship with the Raninidæ. De Haan laid great stress on this point of resemblance between the Leucosiidæ and the Raninidæ, but a detail examination shows that the result is arrived at in a different manner in the two families and must be regarded as a case of homoplasy rather than homogeny. In all the Raninidæ the free end of the sternal plastron is formed by the more or less prominent lanceolate median projection of the tenth (chelipedal) sternum. The ninth sternum is narrow and projects upwards at an angle of  $130^{\circ}$  to  $135^{\circ}$  above the lanceolate projection of the tenth sternum. The coxæ of the third maxillipeds are articulated to the hinder end of the narrow ninth sternum, and therefore close to the median line, and they effectively exclude any part of the sternum from participation in the formation of the broad plastron (see fig. 27, ix). Further, in the Raninidæ, the connection between branchiostegite and plastron in front of the cheliped is effected by lateral outgrowths of the tenth sternum which meet the branchiostegal margin, not by any marked ingrowths of the latter. In the Leucosiidæ (I have studied the arrangement in *Ilia nucleus*, *Philyria undecimspinosa*, and *Philyria levis*) the ninth sternum is short antero-posteriorly, but broad and forms the anterior end of the plastron. The coxæ of the third maxillipeds are articulated to its outer ends and are therefore far apart. The tenth sternum does not give off any prominent outgrowths in front of the chelipeds, but is united to an inwardly directed process of the edge of the branchiostegite on each side, this process being the most anterior of a series of similar downgrowths of the branchiostegal margin which pass between the coxæ of the pereopods and effect the very close and elaborate fit of branchiostegite to coxæ already referred to. It may be mentioned here that A. Milne Edwards and Bouvier (28) have described a shallow pterygostomial gutter closed in below by the third maxillipeds in *Cyclodorippe*. This gutter occupies the same position as the well-known pterygostomial inhalant canal of the Leucosiidæ, and the similarity of the structural appointments is so great as to suggest the derivation of the Leucosiidæ from a Cyclodorippid rather than from a Raninid ancestor.

Finally some importance is to be attached to an apparently minor feature. In all the Oxystomatous Crabs the floor of the exhalant branchial canal is formed by an expanded spoon-shaped operculum furnished by the first maxilliped. In the Raninidæ (see figs. 31, 45, 50, & 53) both the exopodite and endopodite are expanded and modified, and co-operate in forming the operculiform floor in question, but it is the exopodite which is the longest, most expanded, and the most effective agent in forming the operculiform floor of the anterior part of the exhalant canal. This modified exopodite never bears a flagellum. In the Leucosiidæ, the Calappinæ, and the Matutinæ (Garstang is in error in stating that the exopodite is operculiform in *Matuta banksii*) it is the endopodite of the first maxilliped that is elongated.

expanded, and modified to form the operculiform floor of the exhalant canal. The exopodite is somewhat modified and to a varying extent in different genera, but it is always shorter than the endopodite, does not share in the formation of the operculum, on the whole retains the characteristic shape of an exopodite, and invariably bears a flagellum—I hope I may not be criticised for attaching undue importance to a trifling character. It is just such instances as this, in which the same purpose is effected by somewhat different means, that afford the best criteria as to whether some particular structural resemblance is homogenetic or homoplastic. It was the discovery of this difference in the structure of the first maxillipeds that finally confirmed my opinion that the Raninidæ are not genetically connected with the other Oxystomatous Crabs. My reliance on this item of evidence was somewhat shaken by A. Milne Edwards and Bouvier's statement that the opercular floor of the exhalant canals in *Cymonomus* is formed by the dilated exopodites of the first maxilliped, but an examination of their figure (28, pl. xv. fig. 6—there is a mistake in the numbering of these figures—) shows that the resemblance to the Raninidæ is only superficial, and the exopodite of the first maxilliped of *Cymonomus* has a long six-jointed flagellum furnished with long setæ. My test case, therefore, holds good, and the evidence produced is sufficient to justify Boas' doubt as to the inclusion of the Raninidæ among the other Oxystomata, and A. Milne Edwards and Bouvier's decision to exclude them from their monograph on the Oxystomata of the 'Blake' and 'Hassler' Expeditions. The Raninidæ, therefore, must be removed from their present systematic position and assigned to some other place in classification. They cannot be excluded from the section Brachyura for reasons given on p. 27, but in conformity with more recent and generally accepted classifications they must rank as a separate tribe, equivalent to the Dromiacea, Brachygnatha, and the rest of the Oxystomata. For this new tribe I propose the name **Gymnopleura**\*, which directs attention to one of the most characteristic features of the group, namely the exposure of the epimera of the posterior thoracic segments. This new tribe may be defined as follows.

#### Tribe **GYMNOPLEURA.**

Anterior thoracic sterna broad, posterior thoracic sterna narrow and keel-like; posterior thoracic epimera largely exposed by reduction of branchiostegite; female openings on coxæ; last pair of pereopods dorsal in position,

\* Mr. T. R. R. Stebbing in 'Nature,' Jany. 1922, has pointed out that Latreille (Cours d'Entomologie, 1831) instituted the tribe *Notopterygia* for *Ranina*. At first sight it seemed advisable to adopt Latreille's name for the tribe comprising the Raninidæ instead of my own. But the rules of nomenclature do not apply to tribal names; Latreille's system of classification differs largely from that followed in this paper and his reasons for placing *Ranina* in a separate tribe differ widely from mine. Confusion rather than perspicuity would result from the adoption of Latreille's tribal name.

normal or reduced in size; sternal canal present; thoracic nerve ganglion-chain elongate; antennary sternum triangular, spout-shaped; branchiæ 8 on each side. . . . . FAMILY: *Raninidæ*.

We may now deal with some features of general and special interest presented by the tribe *Gymnopleura*. It has been shown to have originated, independently of other "crabs," from the *Astacura*. It is but a small assemblage of animals, comprising some eight or nine living genera, exhibiting a very small range of variation, and evidently very well adapted to their environment, for the tribe emerges in the Cretaceous with its special adaptive characters fully established, and two of the recent genera date back to the Eocene. But although not descended from crabs, but from lobsters, the *Raninidæ* have been so similarly modified, in one direction and another, that they must be classed with the crabs with which they have no relationship save that of a remote common ancestor which was not itself a crab. It is by no means an isolated phenomenon. We know of several crab-like forms, *Porcellana*, *Lithodes*, *Hippa*, and the interesting *Porcellanopagurus*, whose assumption of a crab-like form has been described in a very lively manner by Borradaile (20), which have undoubtedly been derived, quite independently in each individual case, from *Macrurus* ancestors. The question is, what causes have operated to produce so great similarities in animals so remotely related to one another? Without doubt, I think, the answer is that the efficient cause has been the assumption of the habit of burrowing in sand or mud. Bohn (7) has shown that various members of the *Nephropsidea*, when living on sandy bottoms, protect themselves by an investment of sand, and to a limited extent take cover in it. But their pereopods are ill-adapted for digging; they must retreat backwards into the sand to leave their antennæ and eyes free to keep watch against enemies, and the elongated abdomen is a great obstacle to the effective and rapid concealment of the posterior parts of their bodies. A suitable modification of the pereopods and reduction and infolding of the obstructive abdomen are prerequisite to retrofossorial efficiency, and any mutations in these directions must have had a high selective value. It is not surprising that favourable modifications should have presented themselves and have been selected several times over, nor is it surprising that, once the burrowing habit was adopted, similar adaptive modifications to the new condition of life should have established themselves. In the first place the Decapod, buried in sand or mud, must adapt its respiratory mechanism to the changed conditions. The inhalant spaces extending along the posterior and ventral edges of the branchiostegite would be choked and rendered useless unless some provision against the entrance of sand were developed, and the researches of Garstang and Bohn have shown by what various means this form of suffocation is obviated in different genera of the sand-burrowing



crabs. Most commonly the edges of the branchiostegite are fitted closely to the epimera just above the coxæ of the pereopods and to the tergum of the first abdominal segment, so that no water can find ingress or egress that way. As a consequence the podobranchs or arthrobranchs of the three posterior pereopods disappear; there is no longer room for them, and as the branchial cavity is reduced posteriorly by the great development of the muscle-cavities of the digging legs, the posterior pleurobranchs follow suit. The branchiæ are reduced in number and those that remain are massed in the anterior half of the branchial cavity, nearest to the newly developed entrance of the respiratory current in front of the chelipeds. In the Raninidæ, however, the arrangements differ from those usually observed in crabs. There is, in most of them, a pair of posterior respiratory orifices situated between the tergum of the first abdominal segment and the coxæ of the last pair of pereopods. When the abdomen is extended or only slightly flexed, water can pass freely into or out of these orifices, but they are pretty effectively closed when the abdomen is closely flexed under the thorax. The orifices were accurately described and figured in *Ranina* by Milne Edwards, but many subsequent authors, particularly Ortmann (42), seem to have failed to recognise them. Borrodaile (14) gives an accurate account of their relations. These posterior branchial orifices are not, however, peculiar to the Raninidæ: I have found them in precisely the same position in *Corystes*, in which genus they can easily be seen by bending the abdomen upwards and looking between the lower side of the tergum of the first abdominal segment and the coxa of the last pair of legs. Garstang (30) failed to observe these apertures in *Corystes*, and I suspect, but have not yet had the opportunity of proving it by experiment, that they form the main entrance for water into the branchial chamber during the operation of the normal current. There is also a pair of posterior apertures in *Thia polita*, but these are in a somewhat different position, close under the edge of the branchiostegite in front and to the outside of the articulation of the first abdominal segment with the carapace, and well in front of the coxæ of the last pair of pereopods. The persistence of a posterior branchial opening is a primitive feature, never to be seen, as far as my observations go, in crabs in which the abdomen is permanently flexed and kept closely applied to the sternal plastron.

To return to the Raninidæ: the posterior part of the branchial chamber, into which the posterior orifice opens, is reduced to a narrow passage by the reduction in vertical depth of the branchiostegite and the close adherence of its edge to the thoracic epimera. The edge of the branchiostegite is held in place by two prominences, one on the anterior edge of the eleventh, the other on the posterior edge of the thirteenth epimeron, and a close fit is ensured by a well-marked ridge running upwards and backwards along the eleventh, twelfth, and thirteenth epimera (figs. 7 & 17). Thus the entrance of water into or its egress from the branchial chamber at the sides of the

thorax is effectively prevented. The only entrances and exits are by way of the anterior so-called exhalant branchial canals and by the posterior canals described above. Bohn (6) has shown that reversal of the respiratory current, first observed in *Corystes* by Garstang, is a normal phenomenon among Decapod Crustacea, and is manifested even when they are buried in the sand. There must, therefore, be some apparatus in forms which, like the Raninidæ, have posterior branchial orifices for filtering the sand from the water entering by these orifices during the "normal" phase of the respiratory current; that is when it is setting from behind forwards. In most of the Raninidæ, notably in *Ranina*, *Notopus*, *Notopoides*, *Notosceles*, and *Zanclifer*, this apparatus is furnished, partly by the chelipeds, but principally by the manner in which the flattened pereopods, the edges of which are fringed with long and closely set hairs, are bent upwards and forwards in such a manner as to form a water-chamber on either side of the posterior thoracic segments. The part played by the pereopods would never be guessed from the conventional representations of these animals in systematic works, where they are depicted, usually from the dorsal surface, with the legs extended symmetrically on either side of the body in order to display as much as possible of their structure and the chelipeds extended forwards in front of the body. The adaptive characters of the thoracic limbs can be studied with equal advantage in *Notopus*, *Notopoides*, *Zanclifer*, *Notosceles*, and *Ranina*, but I will take the last-named genus as an example for descriptive purposes.

In *Ranina* there is a conspicuous triangular patch of short dense hairs extending forward from the articulation of the cheliped over the postero-lateral area of the pterygostomial region on either side of the thorax. The conjoined basis and ischium of the cheliped is very short and immovably fused to the merus, the two forming a relatively long curved segment of the limb, dilated on its external aspect but smooth and flattened internally so as to fit closely against the hairy patch on the pterygostome. It is evident, from its smooth and polished inner surface, that the ischiomerus is normally held close to the body and slides forwards and inwards or outwards and backwards over the above-mentioned hairy patch. Whatever its position, so long as it is pressed against the hairy patch, there is no room for the passage of water, much less of sand or mud, between it and the pterygostome. When the ischiomerus is rotated as far forward as possible, the somewhat inflated carpus lies beneath the outermost of the large frontal spines of the carapace, and the flattened propodus and dactylus are folded back under the anterior part of the pterygostomial region, but do not fit closely and accurately to the latter as in the case of *Calappa* and *Matuta*. Their function is quite different. It is evident that instead of forming the floor of what Garstang has called an exostegal canal the propodus is so articulated to the carpus that without either the latter or the ischiomerus being shifted from their positions, it can be rotated outwards in such a manner as to rake

sand or other material from beneath the anterior part of the carapace, the raking action being facilitated by the five large spines on the lower margin of the propodus. Thus a more or less clear water-way is kept on the under side of the anterior side of the thorax.

When the ischiomerus is drawn as far back as possible, the carpus can be flexed inwards to form an acute angle with it, and the flattened propodus may then be folded back so far that its posterior margin fits into a groove in the merus and both it and the dactylus are pressed against the basal joints of the third maxillipeds. In this position also the propodus can be rotated outwards with a raking action so as to clear away sand from beneath the body, without any corresponding movement of the ischiomerus and carpus. A close examination of the chelipeds leaves no doubt that their main function is to keep open a passage for water down to their basal joints. From this point backwards water must pass in two streams to the posterior branchial orifices along passages roofed in, partly by the overhanging edges of the branchiostegite, partly by the forwardly directed last pair of pereopods. The inner walls of these passages are formed by the epimera of the eleventh, twelfth, and thirteenth segments, which are somewhat excavated and overhung by the edge of the branchiostegites. Their outer walls are formed by the first three pairs of pereopods, which are tucked up under the roof formed by the last pereopods, the merus in each case being directed forwards, the carpus, propodus, and broad lanceolate dactylus downwards and backwards. The segments of the pereopods being broad and flattened and their margins furnished with fringes of stiff closely set hairs, they form a sort of basket-work or sieve the meshes of which are filled in by the fringes of hairs, and the whole apparatus is adapted to admit to the interior water from which sand and other solid particles have been strained. The strainer is made more effective by the dense hairy fringes on the edges of the branchiostegite, and the whole apparatus is completed and roofed in posteriorly by the flattened segments of the abdomen, which are likewise provided with dense fringes of stiff hairs.

Whatever may be the position of the chelipeds, there is a ventral gap on either side between their basal joints and the first pair of the pereopods. This gap is partly filled by the "epaulettes" projecting from the sterna of the eleventh segment; the rest of the gap is bridged over by the stiff hairs projecting from all round the margins of the epaulettes and forming a very effective strainer. It is through these two gaps furnished with this efficient straining apparatus that the greater part of the respiratory current of water must find its way from the cavity raked out in the sand by the chelipeds underneath the anterior part of the thorax.

The structure and arrangement of the pereopods and their relations to the thoracic epimera and abdomen being as above described, it may be inferred that *Ranina* buries itself in the sand by the digging action of the

first three pairs of pereopods, the fourth pair being used to shovel the displaced sand outwards. When dug in, the animal may be inferred to assume an oblique position, the frontal spines of the carapace just breaking the surface of the sand; the chelipeds are folded up under the pterygostomial region of the carapace and the long three-jointed eye-stalks may be extended well above the sand on the look-out or, on the approach of danger, may be folded back and concealed in the orbital cavities. In this position the normal respiratory current will be provided for by the raking action of the chelipeds and the lateral water-passages enclosed between the pereopods and the thoracic epimera, as described above. These afford a mechanism whereby filtered water is supplied to the posterior branched openings, and the normal exhalant current will pass out by the narrow anterior passage bounded below by the merus of the third maxilliped and laterally by the flattened basal joints of the second antennæ.

As the Raninidæ are tropical and sub-tropical crabs living at considerable depths it has not been possible for me to observe the habits of the living animals, much less to make experiments on their respiratory mechanisms. But in the absence of direct evidence I consider myself justified in giving the foregoing account of the course of the normal respiratory current, the more so because an examination of numerous specimens of *Notopoides latus* and of several examples of *Zanclifer caribensis* in the British Museum of Natural History gives the clearest evidence that these species are sand burrowers, and that an inhalant current passes into their branchial chambers through the posterior branchial orifices, which are exceptionally large and conspicuous in these cases. In nearly all the individuals of these two species the conspicuous hairy fringes of the pereopods, of the abdominal pleura, of the edges of the branchiostegite, and of the epaulettes of the eleventh sterna, are more or less heavily clogged with sand, a fact which bears witness to their function as a filtering apparatus. On the other hand, the water-passages lying between the posterior thoracic epimera and the pereopods, and therefore guarded by these hairy fringes, are remarkably clean and free from sand. The filtration, however, has not been perfect, for the walls of the posterior branchial passages are encrusted with fine particles of sand, the distribution of which leaves no doubt that the current which deposited them set in from behind forwards. The evidence in these two species is remarkably clear, and the inferences drawn from it may be extended to *Notopus dorsipes* and to *Notosceles chimmonis*, though, in the last-named species, in which the last pair of pereopods are greatly reduced in size, there is evidence that the posterior inhalant respiratory current is becoming of less importance and that the incurrent supply of water to the branchial chamber is chiefly provided for by special modifications of the antennary region.

In the absence of opportunities for observation of and experiment on living

animals, the exact course of the anterior inhalant-respiratory current in the Raninidæ must remain largely a matter of conjecture. Nevertheless I have not hesitated to put forward the following interpretation based upon a detailed study of anatomical facts in the hope that, whilst my conclusions must necessarily be subject to revision and correction, naturalists who have opportunities of studying the live animals may be so far interested as to devote some time and trouble to the elucidation of the workings of their respiratory mechanisms. The anatomical characters are most easily studied in *Notopus dorsipes*, and it is probable that what is true of this species is also true of *Ranilia muricata*, M. Edw., but as I have only been able to examine a single dried example of the latter in the British Museum of Natural History, I cannot say anything certain about it. I have stated elsewhere (p. 26) that, in my opinion, *Ranilia*, M. Edw. = *Notopus*, de Haan. In *Notopus* the antennæ are more primitive, that is to say, they depart less from the Macruran pattern, than in any other Raninidæ. The peduncle (figs. 29 & 29a) is made up of five distinct segments of which the proximal is admedian in position, small, largely concealed by the sub-antennary lobe of the pterygostome and bears at its inner angle the aperture of the excretory gland. The second segment is also small and largely concealed by the sub-antennary lobe: it lies on the same level as the first and is external to it. The third segment is large, sub-quadrangular in outline, its extero-ventral surface slightly convex and tuberculated, its intero-dorsal surface smooth and slightly concave. Its admedian margin is prominent and curved, forming a projection which meets its fellow in the middle line. It bears a conspicuous tuft of long forwardly directed setæ. Its extero-anterior angle is produced into a process which embraces the proximal part of the fourth peduncular segment; this process is largely developed in other Raninidæ but remains small in *Notopus*. The fourth and fifth segments are fairly long, their external and ventral surfaces granular and convex, their admedian surfaces smooth and flat or slightly concave. The dorsal and ventral edges of these smooth admedian surfaces are fringed with long closely set plumose setæ which, when the two antennæ are approximated, interlock with the corresponding setæ of the antenna of the other side. The antennary flagellum comprises twenty-six joints, is relatively longer than in any other Raninidæ (except *Ranilia*, M.-Edw. and *Cosmonotus*) and bears a dorsal and a ventral row of strong setæ which are directed obliquely inwards so as to interlock with those of the opposite side when the antennary flagella are approximated. Thus there is formed an antennary water-tube (figs. 1 & 56), shorter indeed but otherwise similar to and fully efficient as that of *Corystes*. Water sucked down the antennary tube passes into a shallow chamber lying behind the bases of the antennæ, the floor of which is formed by the meri of the third maxillipeds, its roof by the spoon-shaped expanded anterior ends of the exopods of

the first maxillipeds. These last are concave dorsally and convex ventrally, and fit so closely and accurately to the converging exhalant channels of the antennary sternum as to constitute an efficient horizontal partition between an exhalant passage above and an inhalant passage below. The incurrent stream of water, taking the more ventral course, must pass right and left along the conduits provided by the grooves on the ventral sides of the exopods of the second maxillipeds; thence under the edge of the inflated pterygostome into the channel which lies parallel to that in which the scaphognathite works, but separated from the latter by the vertical partition formed by the mastigobranch of the first maxilliped. The floor of these inhalant passages is formed by the flat and closely opposed meri and ischia of the third maxillipeds the outer edges of which fit close to the mouth frame. There is no "exostegal" groove in the pterygostome forming a definite inhalant canal as in the Leucosiidæ, but the relation of the incurrent to the excurrent stream of water must otherwise be much the same in the two groups. That is to say, in both cases there must be two opposite currents, the one setting inwards to, the other setting outwards from the antennary region of the front.

In both the Raninidæ and the Leucosiidæ the excurrent stream is set in motion by the "normal" action of the scaphognathite, and passes forward between the converging channels of the antennary sternum and the exopods of the first maxillipeds to emerge between the basal joints of the antennules. The course of the incurrent stream in the Raninidæ is as described above for *Notopus*, but it can hardly have escaped the reader's attention that the channels in which the opposite currents flow are not very distinctly separated from one another. In the Leucosiidæ the existence of the exostegal canals makes the separation much more complete, and the respiratory mechanism is in this respect more highly specialised than it is in the Raninidæ. In this connection it should not be forgotten that the latter have additional apertures of ingress to the branchial chambers, viz., the posterior branchial apertures of which there is no counterpart in the Leucosiidæ.

It may be surmised that *Notopus* makes use of the posterior branchial apertures only when it is lightly covered by the loose upper stratum of sand, and can make use of the raking action of the chelipeds to clear a passage for water below the thorax. As it digs down into the more compact deeper layers of sand, this source of water-supply must become more and more restricted, and the antennary tube is then brought into action. It is of course possible and even probable that, when the antennary tube is used, the action of the scaphognathite is reversed and the posterior branchial apertures become exhalant, the frontal exhalant passages being closed and thrown out of action so long as the respiratory current is reversed, only to be brought into use again when the normal respiratory current, from behind forwards, is restored. But the evidence is strongly in favour of my contention

that in the Raninidæ an anterior incurrent stream of water is produced by the "normal" action of the scaphognathite.

In no other member of the group (with the possible exception of *Cosmonotus*, which I have not had the opportunity of studying sufficiently closely) do the flagella of the antennæ form a water-tube as in *Notopus* and *Ranilia*. Indeed, the antennæ are modified in other directions but, none the less, are subservient to the establishment of an inhalant water current, the course of which can best be described by taking *Ranina* as an example.

In this genus both the antennæ and the antennules are modified in connection with the respiratory currents. The antenna (figs. 35 & 35 a) is short and thick, the flagellum reduced to a rudiment comprising at the most seven joints; often it is missing. The two basal joints of the peduncle are fused together, but the suture between them remains distinct. The first joint is triangular in outline, with the apex directed forward; its admedian basal angle projects inwards and slightly forwards and the excretory aperture is placed somewhat to its dorsal side, in such a position that the excretory products are discharged into the excurrent rather than into the incurrent stream. The two basal joints, which have a very limited movement in the antennary socket, lie directly in front of the sub-antennary lobe of the pterygostome, but the third peduncular segment is flexed inwards to form a somewhat acute angle with them. The shape of the third segment can best be understood by reference to figs. 35 and 35 a, which represent external and admedian views of the right antenna. The most noticeable feature is the great development of the external lobe. Small and inconspicuous in *Notopus*, this lobe in *Ranina* forms a large sinuous ridge which projects forward as far as the anterior limit of the fourth segment; its outer margin is fringed with long plumose setæ. When the third peduncular segment is flexed towards the middle line, the lobe in question is brought into a position athwart the incomplete lower boundary of the orbital cavity, and forms its ventral and internal wall, the long fringe of hairs on what is now its anterior margin extending upwards across the orbital cavity and interlocking with a similar fringe spreading downwards from the supra-orbital ridge of the front of the carapace. For brevity's sake this lobe will be referred to as the crest of the third peduncular segment. The fourth segment is sub-triangular in section: its external and ventral surfaces are convex and granular, but its internal surface is smooth, slightly concave, and flabelliform in outline. Its margins are surrounded with long plumose setæ the disposition of which is shown in fig. 35 a. The fifth peduncular segment is small and the flagellum rudimentary or absent. When the antennæ are flexed inwards, the concave flabelliform surfaces of the fourth segments are brought nearly into contact in the middle line, their marginal setæ interlock, and thus a narrow but deep space is enclosed which is continued posteriorly into the wider space bounded

laterally by the smooth and somewhat concave inner surfaces of the third peduncular segment; ventrally by the meri of the third maxillipeds; dorsally by the densely setose exopods of the first maxillipeds. This may be called the inhalant chamber.

The antennules are inserted to the inside of and somewhat above the antennæ. As shown in figs. 34 and 34 *a*, their basal joints are expanded distally into a flabelliform lobe very similar to that of the fourth peduncular segment of the antennæ and, like the latter, their margins are garnished with a fringe of long setæ. The slightly concave inner surfaces of these flabelliform expansions of the antennules, when opposed in the middle line, form a second vertical cleft or passage within the larger passage formed by the antennæ, and this internal and somewhat dorsal antennular passage is so disposed that its hinder opening coincides with the spout formed by the convergence of the exhalant canals of the antennary sternum. The cleft between the basal joints of the antennules therefore serves as a conduit for the excurrent stream of water. Thus far the apparatus for directing the courses of the excurrent and incurrent respiratory streams differs from that of *Notopus* chiefly in the fact that in *Ranina* the long tube formed by the antennary flagella is absent, but in the latter genus a large part of the incurrent stream must find its way into the above-mentioned inhalant chamber through the orbital cavities. I have already shown how these narrow and elongated cavities are covered in by fringes of setæ which meet over the retracted eyes and eye-stalks but are pushed aside when the latter are extended. Though the orbit appears to be closed below by the crest of the third segment of the antennary peduncle, a sufficiently wide space is left between this segment and the basal joint of the antennule to allow of the free passage of water from the orbit into the inhalant chamber, and much of the inhalant current must pass through the orbits. It is evident that when the animal is deeply dug in, the broad front of the carapace just breaks the surface of the sand; the tips of the largest frontal spines perhaps project very slightly above it. The hairy fringes of the orbits and of the fourth joints of the antennæ are then just awash between sand and water, and are admirably adapted for filtering solid particles from the streams setting inwards through the orbits and between the flabelliform fourth segments of the antennæ. Water is also admitted into the orbits on either side through a considerable cleft lying between the long and narrow sub-orbital lobe of the pterygostome and the innermost of the large frontal spines. These clefts are guarded by dense hairy fringes. The arrangements by which the incurrent stream is directed from the inhalant chamber into the branchial chamber by the channel formed by the exopod of the second maxilliped are the same in *Ranina* as in *Notopus*.

I would not have presumed to give an account unsupported by direct



observation and experiment of such complicated functions as those dealt with in the foregoing paragraphs if there were not very clear evidence that such an anterior inhalant current as I have described does in fact exist. One such piece of evidence is afforded by the matted feltwork of hairs covering the ventral surfaces of the expanded anterior extremities of the exopods of the first maxillipeds. These hairs lie flat and point backwards: they are as evidently laid back by a current of water passing over them as the sea-grass on the mud-banks of an estuary is laid back by the tide that has swept over it. Again, in most examples of *Ranina* a considerable amount of sand is entangled in the setæ with which both the exopods and endopods of the second maxillipeds are abundantly furnished. This gives evidence that these appendages are bathed by a current of water not wholly freed from sand-particles by the filtering apparatus of the orbits and antennæ. But perhaps the clearest evidence of all was furnished by the large *Ranina* sent me by Prof. Kishinoye. In this specimen the inner surfaces of the third peduncular segments of the antennæ, the ventral surfaces of the exopods of the first and second maxillipeds, the inner surfaces of the mastigobranchs of the first maxillipeds, the proximal part of the mastigobranchs of the second maxillipeds, and the bases of the podobranchs of the second and third maxillipeds were infested by numerous small pedunculate cirrhipedes belonging to some as yet undetermined genus and species of the family Lepadidæ. In other words, these intruders had established themselves along what I have described as the course of the incurrent respiratory stream, but none were to be found in the upper part of the gill-chamber, nor on the scaphognathite, nor on any part of the walls of the exhalant canals. It is evident that their larvæ had been swept by the incurrent stream into the inhalant chamber, and had subsequently fixed themselves in positions where the adults could obtain a constant supply of nourishment borne by the incoming current. But, where the currents were setting outwards, conditions were unfavourable and none had established themselves.

From what precedes, it follows that *Ranina*, no less than *Notopus*, is highly adaptable in respect of its respiratory arrangements, and can make use of different mechanisms as the circumstances of the moment may require. When half buried in loose sand or when wandering on the surface these animals probably respire through the apertures at the posterior end of the thorax. When deeply buried in compact sand they are forced to rely on the antennary apparatus. In point of efficiency and specialisation their respiratory mechanisms fall far short of those exhibited by other "Oxystomatous" crabs, the Leucosiidæ, the Calappinæ, and the Matutinæ, but adaptability to varying conditions implies a high survival value, and it is to be remarked that *Notopus* and *Ranina* are among the oldest of the fossil Raninidæ.

Among other genera, *Zanclifer* and *Notopoides*, though their antennary flagella are not so much reduced, are in all essential respects so similar to *Ranina* that it can hardly be doubted that they have similar habits and are equally adaptable as regards their respiratory processes. *Zanclifer* differs from all other Raninidæ in having normal, *i. e.* not feathered and differentiated, chelipeds, and it may be that it is more nearly related to the ancestral form than *Notopus*. It has all the external characteristics of a burrowing crab. *Notopoides*, on the other hand, is much more closely related to *Notopus*, from which it differs mainly in the elongation of the twelfth sternum, whereby the second, third, and fourth pereopods are shifted backwards and form a posterior group of legs, separated by a space from the first pereopods: this feature is exhibited to a more marked degree in *Notosceles* (fig. 3) and is carried to an extreme in *Raninoides* (fig. 6). In each genus the increase in length of the twelfth sternum is correlated with a reduction in size of the last pair of pereopods, a progressive narrowing of the abdomen, a reduction in the size and functional importance of the posterior branchial orifices, and progressive modifications of the second and third pereopods indicative of their increasing use as swimming organs. A comparison of the series *Ranina*, *Notopus*, *Notopoides*, *Notosceles*, *Raninoides*, leads me to the conclusion that, whilst all of them are to a greater or less extent sand-burrowers, the first-named during its periods of activity progresses mainly by crawling and is a poor swimmer. *Notopus* and *Notopoides* crawl and swim; *Notosceles* is a fairly efficient and *Raninoides* a very efficient swimmer. This conclusion I will now endeavour to justify.

*Notopoides* is obviously a burrowing crab; the sandy condition of the specimens in the Natural History Museum bears testimony to this habit. In most of the structural features subservient to the respiratory processes *Notopoides* bears a strong resemblance to *Notopus*. Attention may be directed specially to the following points: the last pair of pereopods are not much reduced in size and all their joints are densely fringed with hairs; the tergum of the first abdominal somite is as broad as the posterior margin of the carapace; the posterior branchial orifices are patent and give evidence of their function as inhalant passages; the exposed portions of the epimera of the eleventh, twelfth, and thirteenth somites are concave and overhung by the edge of the branchiostegite; the chelipeds are adapted for raking sand from under the thorax. In short, all the adaptations described in *Notopus* and *Ranina* for maintaining a respiratory current through the posterior respiratory orifices are present to an equal degree in *Notopoides*. This genus must be equally addicted to the burrowing habit, but the articulations and characters of its last three pairs of pereopods suggest that, when active, it is to some considerable extent a swimmer.

In *Notosceles* the adaptations for maintaining a posterior inhalant respiratory current are still recognizable, but are obviously less efficient.

The last pair of pereopods, though much reduced in size, is sufficiently liberally provided with hairy fringes to form an effective covering for the roof of the water-chambers enclosed between the other pereopods and the thoracic flanks. The epimera forming these flanks, however, are not so deeply concave as in *Notopoides*, and the posterior branchial orifices, though distinct enough, are smaller and obviously of less functional importance. The dactylus of the last pair of pereopods is small, elliptical, and clearly better adapted for natation than for digging.

Before entering into a discussion of the transition from digging to swimming limbs it should be premised that in the pereopods of all the Raninidæ the articulation of the dactylus to the propodus is singularly like that of the tarsi of the whirligig-beetle *Gyrinus*, familiar to all naturalists from the illuminating description of Miall. Generally, in the Raninidæ, the carpus is moderately long, triangular in shape, with an extensive basal articulation for the propodus. The propodus is a short and broad oblong, more or less flattened, with a very small articulation for the dactylus close behind its postero-external angle. The dactylus is very variable in shape. Generally in the first two pereopods it is lanceolate and obviously efficient in digging, but in the last two pereopods something between crescentic and cleaver-shaped like an oriental "kukri." In either case it is so articulated by a narrow pedicle to one end of the oblong propodus that it can be slid behind the latter as the sticks of a lady's fan slide over one another. A very similar form of limb with yet more elaborate adaptive details is seen in *Matuta* which, like the Raninidæ, is at once a swimming and a burrowing crab. It is presumed that the lanceolate form of dactylus is more useful as a pick, the kukri-shaped dactylus as a shovel, but the latter may be serviceable in swimming, just as a shovel may on emergency be used as a paddle. In *Zanclifer* the dactyli of all the pereopods are narrow and sickle-shaped; they seem ill adapted for swimming but effective instruments for digging. The criterion for deciding whether a limb is utilised for swimming or for digging consists in the length and mobility of its joints. The short strong limbs of *Ranina* showing restricted mobility at the joints are clearly fossorial and ill adapted for natation: the somewhat longer and more mobile limbs of *Notopus* and *Notopoides* are, however, serviceable for both purposes. In *Notosceles* (figs. 2 & 3) the dactylus of the second pereopods is sickle-shaped as in *Zanclifer*, and it may be inferred that this pair of limbs is specialised for digging, but it can hardly be doubted that the broad kukri-shaped dactylus of the third pair, hinged fanwise to the outer angle of the transversely elongated propodus and provided with a marginal fringe of long setæ, is specially adapted for swimming. The reduced fourth pereopods of this genus, with their small flat elliptical dactyli, can hardly be of any value in digging and are rather suggestive of steering paddles.

Though *Notosceles* is in several respects intermediate between *Notopoides* and *Raninoides*, the last-named genus (figs. 5 & 6) has many distinctive features, most of which may be explained as adaptations to a swimming habit. The carapace is elongated, and its flanks taper so evenly posteriorly that it may fairly be described as boat-shaped. The first abdominal tergum is notably narrower than the posterior margin of the carapace, and the whole abdomen is narrow and more distinctly flexed under the thorax than is usual in Raninidæ. On the ventral surface there is a broad and long flat plastron in the formation of which the eleventh and twelfth sterna take an even larger share than the tenth (fig. 6). The twelfth sternum is of considerable length antero-posteriorly and is also broad and nearly flat. The articular cavities of the second pair of pereiopods are placed at its hinder border and face backwards. The thirteenth sternum being very short, the articular cavities of the third pereiopods are close to those of the second, and the two pairs of limbs, whilst closely contiguous to one another, are separated by the whole length of the twelfth sternum from the first pereiopods. The last pair of pereiopods are so reduced and slender that they are usually described as fili-form; they terminate in minute pointed dactyli. The reduction of the last pair of legs and the narrowing of the base of the abdomen seems to be correlated with the suppression of the posterior branchial orifices; at any rate, I can find no trace of these orifices in *Raninoides*. Nor could they be of much service if present, for the external water conduits which in other forms admit of a flow of filtered water to these orifices are here wanting. Though the eleventh, twelfth, and thirteenth thoracic epimera are as much exposed to the surface in *Raninoides* as in other Raninidæ, they are not concave and are scarcely overhung by the edge of the branchiostegite. The epimeron of the eleventh somite is relatively small, and so far from being concave that it is slightly convex. The epimera of the twelfth and thirteenth somites are obliquely grooved, and into these grooves the meri of the second and third pereiopods, when bent forwards and pressed against the sides of the body, fit so closely that no water can pass between. The first pair of pereiopods are slender, and when at rest are directed forwards, their large cordate dactyli being pressed against the bases of the chelipeds. Their function is obscure, but probably they are used for digging. The characters of the second and third pereiopods are clearly shown in fig. 6. In these limbs the coxa and basis are directed backwards: the short ischium is nearly transverse to the long axis of the body: the merus is long and slender: the carpus normal, but it is to be observed that both it and the merus are scantily furnished with short hairs. The propodus and dactylus are flat and greatly expanded and the "fan-hinge" between them is a noticeable feature. A fringe of long stiff hairs is borne on the hind edge of the propodus and on the inner margin of the dactylus. The

efficiency as organs of natation of these broad blades borne at the end of slender and very mobile limbs is apparent. Evidently *Raninoides* is a strong swimmer and, a poor digger, and as such stands at the end of the series opposite from *Ranina*. As the posterior branchial orifices are absent, one might expect to find special arrangements for an incurrent respiratory stream in the frontal region, but, though I have looked carefully for such, I have been quite unsuccessful. However, I will deal with this question further on.

*Lyreidus* (fig. 4) exhibits so many resemblances to *Raninoides* that one can hardly doubt that the two are closely related, yet, as I shall show, they are clearly adapted to different conditions of life. In *Lyreidus* the abdomen is narrow; its first three segments lie nearly in a straight line with the carapace, but the fourth is of peculiar shape, bears a strong median dorsal spine, and constitutes as it were the knuckle of a sharp ventral flexure. The sixth abdominal segment is long and narrow; its posterior angles are produced into small aliform processes which at first sight might be mistaken for vestigial uropods, but they are only processes of the tergum having on their ventral surfaces small concavities which, when the abdomen is flexed to its fullest extent, engage with small knobs on the two pterygoid processes extending backwards from the twelfth sternum. No such apparatus for locking the flexed abdomen to the sternum is seen in any other Raninid. The last pair of pereopods are so slender that, like those of *Raninoides*, they may be described as filiform: they terminate in small flattened elliptical dactyli. Correlated with the reduction of the abdomen and of the last pair of pereopods is the absence of posterior branchial orifices. I have studied this point carefully and am certain that these orifices are non-existent in *L. tridentatus*, nor could I find any trace of them in the large specimen of *L. channeri* in the Natural History Museum. As there are no posterior respiratory orifices the water conduits of the flanks are, as might be expected, absent. The epimera of the posterior thoracic somites are nearly flat and the edge of the branchiostegite is but slightly prominent and bare of setæ. In the frontal and oral regions there are also many points of resemblance. Though the "front" is truncated and scarcely narrower than the broadest part of the carapace in *Raninoides*, the distance between the extra-orbital spines and the lateral spines shows that this region has undergone elongation. Further examination shows that it is the antennary somite that has been lengthened, for the antennary sternum, which has more or less the shape of an equilateral triangle in *Notopus* and *Notosceles*, is an isosceles triangle in *Raninoides*. In *Lyreidus* the elongation of the antennary somite is carried to an extreme, and the front being narrowed, the fore part of the carapace is produced into the snout characteristic of the genus, the lateral spines being situated far behind the orbits. As I shall show further on, the details of the

antennules and antennæ are extraordinarily similar in *Raninoides* and *Lyreidus* (figs. 36-39) ; so also are details in the first and second and even in the third maxillipeds. In all these things the relationship seems very close, but in other respects the two forms are divergent. In *Lyreidus* the eleventh sternum is large but narrowed between the articulations of the first pereopods and produced backwards into two small pterygoid processes which form the sides of a hollow in which the last segment of the abdomen can be lodged, as described above. Owing to the presence of these pterygoid processes the twelfth sternum appears to be deeply fitted, but it is really short, narrow, and flat, in this differing much from *Raninoides*. The thirteenth sternum being also short the coxæ of the first three pairs of pereopods are close together, and in this respect *Lyreidus* resembles *Notopus* rather than *Notopoides*, *Notosceles*, or *Raninoides*. In the first and second pereopods of *Lyreidus* the ischiomerus is long, slender, and scantily fringed with hairs ; the carpus rather short ; the propodus nearly twice as long as it is broad ; the dactylus elongate and almost styliform, with a strong external ridge. In the third pereopods the propodus is about as broad as it is long and the dactylus cultriform. These are clearly digging and walking legs, and one may conclude that the descendants of a form in which reduction of the abdomen and last pair of legs led to the suppression of the posterior branchial orifices, diverged as they adopted a more exclusively swimming habit into *Raninoides*, as they became more exclusively burrowers into *Lyreidus*. *Lyreidus* must bury itself deeply, with the tip of its narrow elongated snout just breaking the surface of the sand. Having no posterior branchial orifices it must be dependent on an inhalant current setting in somewhere in the region of the snout. One would expect some specialised inhalant apparatus, but there is very little evidence of such. Indeed, it is a singular thing that *Ranina*, *Notopus*, and *Notosceles*, all of which have well-developed posterior branchial orifices, have in addition much more specialised orbital and antennary arrangements for directing the flow of an incurrent respiratory stream than have *Raninoides* and *Lyreidus*, in which posterior respiratory orifices are absent. In *Notosceles* the antennary structure is not very different from that of *Ranina*. The flagellum is longer (figs. 41 & 41a), but the thick shortened segments of the peduncle, the flabellate shape of the fourth joint with its fringe of plumose hairs, the greatly developed crest of the third joint also fringed with hairs, are very similar. So also is the flabellate shape of the basal joint of the antennules. Fig. 57 is a frontal view of the "face" of *Notosceles* showing the antennæ as nearly as I can draw them in their natural position. In the centre, below the rostrum, is the narrow exhalant passage bounded by the basal joints of the antennules. The orbits are closed below by the crests of third segments of the antennary peduncles, and the spaces below are filled in by the proximal segments of the antennæ which in

their turn are overlapped by the broad anterior margins of the meri of the third maxillipeds. The left antenna is closed nearly as far as it will go against the antennule, and this is the more normal position: that of the right side (the spectator's left) has been pulled outwards to show the passage between the third and fourth joints of the antennary peduncle and the basal joint of the antennules. Through this passage water can pass from the orbits to the inhalant chamber covered in below by the meri of the third maxillipeds. The arrangements are very much the same as in *Ranina* though somewhat less highly specialised. In *Raninoides* (figs. 36 & 37) and *Lyreidus* (figs. 38 & 39) the basal joints of both antennules and antennæ are longer and more slender, and to that extent more primitive than in *Notosceles* and *Ranina*. In the antennules the admedian surfaces of the basal joints of the antennules are expanded and somewhat concave, so that when opposed they form a conduit for the exhalant current. The third segment of the antennary peduncle is long; a good deal longer in *Lyreidus* than in *Raninoides*. The crest is prominent but narrow, and extends nearly as far forward as the end of the fourth segment. The proportions differ slightly in the two species, but the general character is the same. The nature and distribution of the hairy fringes are clearly shown in the drawings. The relative positions of the antennules and antennæ are shown in fig. 58 for *Raninoides*: they are hardly different in *Lyreidus*. It will be observed that the "spout" of the antennary sternum is produced to open well forward between the basal joints of the antennules: it hardly extends as far forward in *Lyreidus*. In both genera, but to a greater extent in *Lyreidus* than in *Raninoides*, the third peduncular segment of the antenna is overlapped by the tip of the elongated merus of the third maxillipeds, and the portion not overlapped is covered by a tuft of long hairs projecting forward from the tip of the merus. The inner faces of the third peduncular segments of the antennæ and their crests are so shaped that when bent inwards they fit very exactly to the outer surfaces of the basal joints of the antennules, and when in this position completely bar the passage of water from the orbits to the inhalant chamber above the third maxillipeds. But when the antennæ diverge slightly outwards a clear passage is left between the antennules and the antennæ, and the intrusion of sand is guarded against by the overlapping bristles of both. Through this passage, I think, the inhalant current must pass when the scaphognathite is working normally, and through it the excurrent stream must flow when the action of the scaphognathite is reversed. But the subject is very obscure, and I am by no means content with this explanation. I give it for what it is worth in the hope that some favourably placed naturalist may read it, find fault with it, and straightway proceed to make observations and experiments on the living animals. The results cannot fail to be of interest. I feel certain only of this, that there is an inhalant current between the third and

the second and first maxillipeds. It is to direct this current under the edge of the mouth frame into the branchial chamber that the exopod of the second maxilliped is elongated and modified by being channelled along its ventral surface. The modification is carried furthest in *Notosceles* (fig. 44) and *Ranina* (fig. 42), two forms in which the accessory antennary modifications are highly developed, and in these the exopod has lost its flagellum. But in *Notopus*, in which genus the antennæ are most highly specialised for respiratory purposes, the exopod in question (fig. 32) retains a large flagellum, and the flagellum is present but small in *Lyreidus* (fig. 52) and *Raninoides* (fig. 49). This may seem a trivial character, but it gains importance when comparison is made with the same appendage in the Leucosiidæ. In *Philyra lævis* for example (fig. 54) the exopod of the second maxilliped is of simple shape, shorter than the endopod and convex ventrally. In this species, as in all the Leucosiidæ, there is a definite exostegal canal covered in below by the exopod of the maxilliped: the second maxilliped, therefore, does not lie in the course of the incurrent stream and is not modified. I have already (p. 54) called attention to the difference between the first maxillipeds of the Raninidæ and those of other Oxystomatous crabs. Indeed, as I have already indicated when dealing with the endophragmal skeleton, the anterior thoracic sterna, and other structures, the Leucosiidæ differ in a hundred ways from the Raninidæ, and I regard the comparison with *Lyreidus* as wholly illusory. The exostegal canal of the Leucosiidæ is most probably derived from the shallow groove in the pterygostome occupying the same position in *Cyclodorippe*. It would be interesting and not wholly irrelevant to attempt to trace out the various lines of descent in the families of Oxystomata other than the Raninidæ, and I have collected much evidence on this subject based on a study of the endophragmal skeleton and other anatomical features not taken into account by M. Edwards and Bouvier. But it would almost double the length of this memoir if I were to make the attempt. I have already written enough, and have, I hope, proved my main thesis that the Raninidæ cannot have descended, by way of the Dorippidæ and the Dromiacea, from the Macrura. They have originated independently from the last named, and must therefore be separated from other Oxystomes as a separate tribe Gymnopleura. I have endeavoured to show that the numerous brachyuran features exhibited by this tribe must be explained by their having adopted the same habits as other crabs, and that such modifications as the reduction of the abdomen; the loss of the uropods; the adherence of the branchiostegite to the thoracic epimera (exhibited, however, in a quite peculiar manner in the Gymnopleura); the expansion of the ischium and merus of the third maxillipeds; the broadening of the front, with which is correlated the formation of orbital cavities and the reduction of the rostrum; the great development of the muscle-cavities of the thorax,—are all characters of high survival value in decapods which have acquired the habit



of burrowing in the sand for protection and concealment. A decapod crustacean which habitually passes a large part of its existence buried in the sand, must undergo a considerable modification of its respiratory arrangements, and I have attempted to give an intelligible account of these modifications in the various members of the Gymnopleura. In the end they lead, as is natural enough, to the suppression of the inhalant current at the hind end of the thorax and to the substitution of inhalant currents in the antennary region. I have said, in the earlier part of this memoir, that the Gymnopleura are crabs *by definition*. They retain so many Macruran features that they cannot be said to be crabs by ancestry, and there is one small Macruran feature which I have omitted to mention before because I only recognised it when the greater part of this paper was written. The statocyst, usually closed in the Brachyura, is open in the Gymnopleura. Certainly so in *Ranina*, *Notosceles*, and *Lyreidus*, but I have not been able to satisfy myself of the existence of the aperture in all the species examined because the antennules are very small and I have not been able to cut sections. The position of the aperture of the statocyst is clearly shown in fig. 34 for *Ranina*.

I must conclude with a description and definition of the new genus and species *Notosceles Chimmonis*.

There can be little doubt that *Raninoides serratifrons* of Henderson (36) belongs to the genus *Notosceles* and not to *Raninoides*, but his species, from Ceylon, is different to mine. He mentions another example of *serratifrons* from Holothuria Bank, N.W. Australia, as being in the collections of the British Museum of Natural History, but I was unable to find it there. There are considerable differences between *Notosceles* and *Raninoides*, many of which have been referred to in the course of this paper.

#### NOTOSCELES, nov. gen.

Carapace ovate, convex from side to side, minutely punctate or smooth for the most part but granular towards the frontal region; fronto-orbital border little more than half as wide as the broadest part of the carapace; the frontal region marked off by a slight transverse ridge joining the bases of the extra-orbital spines; the rostrum pointed, fairly prominent with two flat lateral and basal teeth. Ocular peduncles rather short, their terminal joints inflated, their corneæ of moderate size. Antennal peduncle short and broad, the flagellum small. Merus of the third maxilliped little more than half as long as the ischium. The second and third sternal elements of the sternal shield (sterna xi & xii) broad and convex in front, but narrowed posteriorly so that the bases of the first as well as the second pereopods are approximated to the middle line. Last pair of pereopods reduced in size, situated above and in front of the penultimate pair, their dactyli small, oval,

and flattened. First abdominal tergum not much narrower than the posterior margin of the carapace, about equal in breadth to the second tergum, the remaining terga progressively narrower; the telson small and triangular.

*NOTOSCELES CHIMMONIS*, n. sp. (Pl. 4. figs. 2 & 3.)

Carapace minutely punctate to smooth over the greater part of its surface, but granular towards the frontal region: proportion of length to breadth of carapace about 5 : 3. The frontal region is marked off by a distinct transverse ridge joining the bases of the extra-orbital spines. The median frontal region is fairly broad and produced anteriorly into a median pointed rostral spine at either side of the base of which is a triangular flattened and somewhat upturned spine, the margins of all three spines minutely serrated. On either side a fissure separates the median frontal projection from a short triangular tooth or spine, and outside the latter is a prominent incurved extra-orbital spine. A single lateral spine occurs on either side of the carapace a short distance behind the extra-orbital spine, and nearly of the same size as the latter. On the upper surface a slight carina runs from the median rostral spine to the transverse granular ridge separating the fronto-orbital region from the rest of the carapace. In the chelipeds the anterior edge of the ischium is serrated; the merus largely dilated externally at its base; the carpus granular above and without a distal spine; the propodus bears two subequal spines on its lower margin, and on its upper surface are two parallel ridges separated by a narrow groove; the immobile claw bears four denticles on its inner margin. In the third maxillipeds the relative length of the merus to the ischium is as 6 : 10; the lower surface of the merus is granular and hairy. The pterygostomial regions are hairy. In the sternal region the chelipedal sternum is of the shape characteristic of the Raninidæ, the following sternal element flat, broad in front and narrow posteriorly; the third element of the sternal plastron triangular, convex, the apex of the triangle anterior. The articular cavities of the first and second pereopods approximated to the middle line. The first abdominal tergum is flat and quadrangular, not much narrower than the posterior margin of the carapace; the second abdominal tergum is nearly equal to it in width; the remaining abdominal terga narrow rapidly and the telson is small and sub-triangular in shape.

Two specimens from the Sulu Sea, both males. Length of the larger specimen with the abdomen fully extended 28 mm.: length of carapace 20 mm.: greatest width of carapace 13 mm.

The species is named after Captain Chimmo, R.N., of H.M.S. 'Nassau,' whose collections from the Sulu Sea were presented to the Oxford University Museum in 1872.

I am of the opinion that *Raninoides serratifrons*, Henderson (36) should

be placed in the genus *Notosceles*, which differs from *Raninoides* in the proportions of the carapace, the shape of the rostrum, the lesser width of the fronto-orbital region, the larger corneæ of the eyes, the proportions of the joints of the antennal peduncles, and in other characters, but especially in the relatively much greater width of the base of the abdomen, and the proportions and shape of the sternal shield.

## LITERATURE.

1. ALCOCK, A.—Natural History Notes from H.M. Indian Marine Survey Steamer 'Investigator.' Ser. ii. no. 1. Ann. Mag. Nat. Hist. (6) xiii. 1894, p. 466.
2. Ibid. Materials for a Carcinological Fauna of India. Journ. Asiatic Soc. Bengal, lxx. 1896, p. 134.
3. BITTNER, A.—Beiträge zur Kenntniss tertiärer Brachyuren Formen. Denkschr. Kais. Wiss. xlviii. 1853.
4. BOAS, E. V.—Studier over Decapodernes Slaegtskabsforhold. Kong. Danske Videnskab. Skrifter, i. Copenhagen, 1880–85.
5. BOHN, G.—Sur la respiration du *Carcinus mænas* Leach. Comptes Rendus de l'Acad. Sci. cxxv. 1897, p. 441.
6. Ibid. Sur la renversement du courant respiratoire chez les Décapodes. *Loc. cit.* cxxv. 1897, p. 539.
7. Ibid. De l'enfouissement chez les Homaridés et les Thalassinidés. *Loc. cit.* cxxvii. 1898, p. 781.
8. BORRADAILE, L. A.—A series of papers in Professor J. Stanley Gardiner's 'Fauna and Geography of the Maldive and Laccadive Archipelagos,' including:—  
Land Crustaceans. Vol. i. pt. 1.
9. Marine Crustaceans: Introduction. Vol. i. pt. 2.
10. Varieties in the Decapod Crustaceans. Vol. i. pt. 2.
11. Portunidae (Swimming Crabs). Vol. i. pt. 2.
12. The Xanthidae and some other Crabs. Vol. i. pt. 3, p. 237.
13. Some Remarks on the Classification of Crabs. Vol. i. pt. 4, p. 424.
14. The Crabs of the Catametope families. Vol. i. pt. 4, p. 429.
15. The Sand Crabs (Oxystomata). Vol. i. pt. 4, p. 434.
16. The Sponge Crabs (Dromiacea). Vol. ii. pt. 1, p. 574.
17. The Spider Crabs (Oxyrhyncha). Vol. ii. pt. 2, p. 681.
18. On the Classification and Genealogy of the Reptant Decapods. Vol. ii. pt. 2, p. 690.
19. The Hippidea, Thalassinidea, and Scyllaridea. Vol. ii. pt. 3, p. 750.
20. Ibid. Crustacea. Pt. I. Decapoda. Brit. Antarctic (Terra Nova) Exped. 1910. Nat. Hist. Rep. Zool. vol. iii. 1916, p. 75.
21. Ibid. Crustacea. Pt. II. *Porcellanopagurus*: an instance of Carcinization. *Loc. cit.* vol. iii. 1916, p. 111.
22. BOUVIER, E. L.—Le système nerveux des Crustacés Décapodes. Ann. Sci. Nat. Zool. (7) vii. 1889, p. 73.
23. Ibid. Sur l'origine homarienne des Crabes. Bull. Soc. Philomath. Paris, (8) viii. 1895, p. 1.
24. CALMAN, W. T.—Crustacea in Ray Lankester's 'Treatise on Zoology.' London, 1909.
25. DANA, J. D.—U.S. Exploring Expedition: xiii. Crustacea.
26. EDWARDS, H. MILNE.—Histoire Naturelle des Crustacés, 3 vols. Paris, 1837.
27. Ibid. Crustacea in Cuvier's 'Règne Animal.'

27. EDWARDS, ALPHONSE.—Note sur l'existence de Crustacés de la famille des Raniniens pendant la période Crétacée. Comptes Rendus, lv. 1862, p. 492.
28. EDWARDS, A. MILNE, and BOUVIER, E. L.—Report on results of dredging by U.S. Survey Steamer 'Blake,' xxxix. : Les Dromiaïés et Oxystomes. Mem. Mus. Comp. Zool. Harvard, xxvii, 1902.
29. Ibid. Exped. Sci. du 'Travailleur' et du 'Talisman': Crustacés Décapodes. Brachyures et Anomures. Paris, 1900.
30. GARSTANG, W.—The habits and respiratory mechanism of *Corystes cassivelaunus*. Jour. Mar. Biol. Assoc. iv. 1896, p. 223.
31. Ibid. On some Modifications of Structures subservient to Respiration in Decapod Crustacea which burrow in the sand. Quart. Journ. Micr. Sci. xl. 1897, p. 211.
32. Ibid. The Function of Antero-lateral Denticulations of the Carapace in Sand-burrowing Crabs. Journ. Mar. Biol. Assoc. iv. 1896, p. 396.
33. Ibid. The Systematic Features, Habits, and Respiratory Phenomena of *Portunus nasutus*. Journ. Mar. Biol. Assoc. iv. 1896, p. 402.
34. HAAN, W. DE.—Crustacea in Siebold's 'Fauna Japonica.' 1850.
35. HENDERSON, J. B.—Report on the Anomura: 'Challenger' Reports, Zoology, xxvii. 1888.
36. Ibid. A Contribution to Indian Carcinology. Trans. Linn. Soc. Lond., Zool. (2) v. 1893, p. 408.
37. HERRICK, F. H.—Natural History of the American Lobster. Bull. Bureau of Fisheries, xxxix. 1911.
38. HUXLEY, T. H.—The Crayfish, an Introduction to the Study of Zoology. London, 1880.
39. IHLE, J. E. W.—Decapoda Brachyura der 'Siboga' Expedition: iii. Oxystomata. Monogr. xxxix b<sup>2</sup>. Leiden, 1918.
40. LAURIE, R. D.—Reports on the Marine Biology of the Sudanese Red Sea: Brachyura. Journ. Linn. Soc., Zool. xxxi. 1915, p. 407.
41. ORTMANN, A.—Die decapoden Krebse des Strasburger Museums. Zool. Jahrb. Abth. f. Systematik, vi. 1892.
42. Ibid. Crustacea in Bronn's 'Thierreich.' 1901.
43. RATHBUN, MARY J.—Marine Brachyura. Rep. Percy Sladen Expedition, vol. iii. 1912, p. 191.
44. WHITE, ADAM.—Short descriptions of new or little-known Decapod Crustacea. Proc. Zool. Soc. 1847, p. 227.

## EXPLANATION OF PLATES 4-7.

## LETTERING.

*A*<sub>1</sub>. Antennules. *A*<sub>2</sub>. Antennæ. *abr.* arthrobranch. *ad.* apodeme. *aph.* arthro-phragm. *at.* antennal respiratory tube. *bst.* branchiostegite. *cr.* crest of antenna. *edpl.* endopleurite. *edst.* endosternite. *en.p.* endopodite. *Ep.* Epimeron. *ep.ad.* epimeral apodeme. *epl.* epaulette of the tenth sternum. *ex.* excretory pore. *exp.* exopodite. *g.* ganglia of nerve chain. *lb.* labrum. *mbr.* mastigobran. *md.* mandible. *oc.* ocular peduncle. *oc.t.* tergum of the ocular segment. *æ.* œsophagus. *P.* Pereiopods. *pbr.* podobran. *pyt.* pterygostome. *plbr.* pleurobranch. *R.* Rostrum. *sbr.* rudimentary setobran. *scy.* aperture of statocyst. *spd.* strophidium. *spng.* strophingium. *st.a.* sternal artery. *st.c.* sternal canal.

The roman numerals refer to segmental structures, sterna, epimera, ganglia, etc. Intersegmental structures are indicated thus ix/x.

## PLATE 4.

- Fig. 1. Ventral view of *Notopus dorsipes*, de Haan. The chelipeds have been turned outwards and the pereiopods are extended to show their structure as far as possible.
- Fig. 2. Dorsal view of *Notosceles chinmonis*, nov. gen. et sp. The chelipeds and pereiopods have been extended as in fig. 1.
- Fig. 3. Ventral view of *Notosceles chinmonis*.
- Fig. 4. Ventral view of *Lyreidus tridentatus*, de Haan. Note the elongated digging dactyli of the first and second pereiopods.
- Fig. 5. Dorsal view of *Raninoides personatus*, White MS., Henderson. The first and third pereiopods of the left side are missing.
- Fig. 6. Ventral view of the same specimen as fig. 5. Note the large size of the sternal plastron, due to the great enlargement of sternum xii and the adaptation of the second and third pereiopods for swimming.
- Fig. 7. Left side view of *Notopus dorsipes*. The first three pairs of pereiopods have been pulled downwards to show the large extent of epimera xi and xii left uncovered by the edge of the branchiostegite.
- Fig. 8. Central nervous system of *Ranina dentata*. i. ocular, ii. antennular, iii. antennary nerves; iv. mandibular nerves; v-ix. nerves to maxillæ and maxillipeds issuing from the subesophageal ganglion; x. ganglion of cheliped; xi-xiv. ganglia of the four posterior thoracic segments; xv-xx. ganglia of the abbreviated abdominal nerve chain. *st.a.* aperture for passage of the sternal artery.
- Fig. 9. Right half of the endophragmal skeleton of *Ranina dentata* as seen from within after division into two halves by a sagittal cut. The more anterior thoracic somites are omitted. The thoracic portion of the central nervous system is shown *in situ*. \*Note the great depth of the sagittal apodemes of sterna xii, xiii, and xiv. *g.* 11-g. 14, the four posterior thoracic ganglia.
- Fig. 10. Central nervous system of *Lyreidus tridentatus*. Lettering as in fig. 8.
- Fig. 11. A drawing from the left side of the eleventh and twelfth segments of the common lobster to show the relations of the endophragmal to the exoskeleton. xi and xii. sterna of the eleventh and twelfth segments. The preparation has been slightly tilted to the right to show the endopleurites *edpl.*, consequently the epimera *Ep.* xi and *Ep.* xii are foreshortened.
- Fig. 12. A left side view of the thoracic skeleton of *Dromia vulgaris*. The ventro-lateral projections of the sterna have been omitted, and the preparation is slightly tilted over to the right. xi-xiv. the four posterior thoracic sterna.

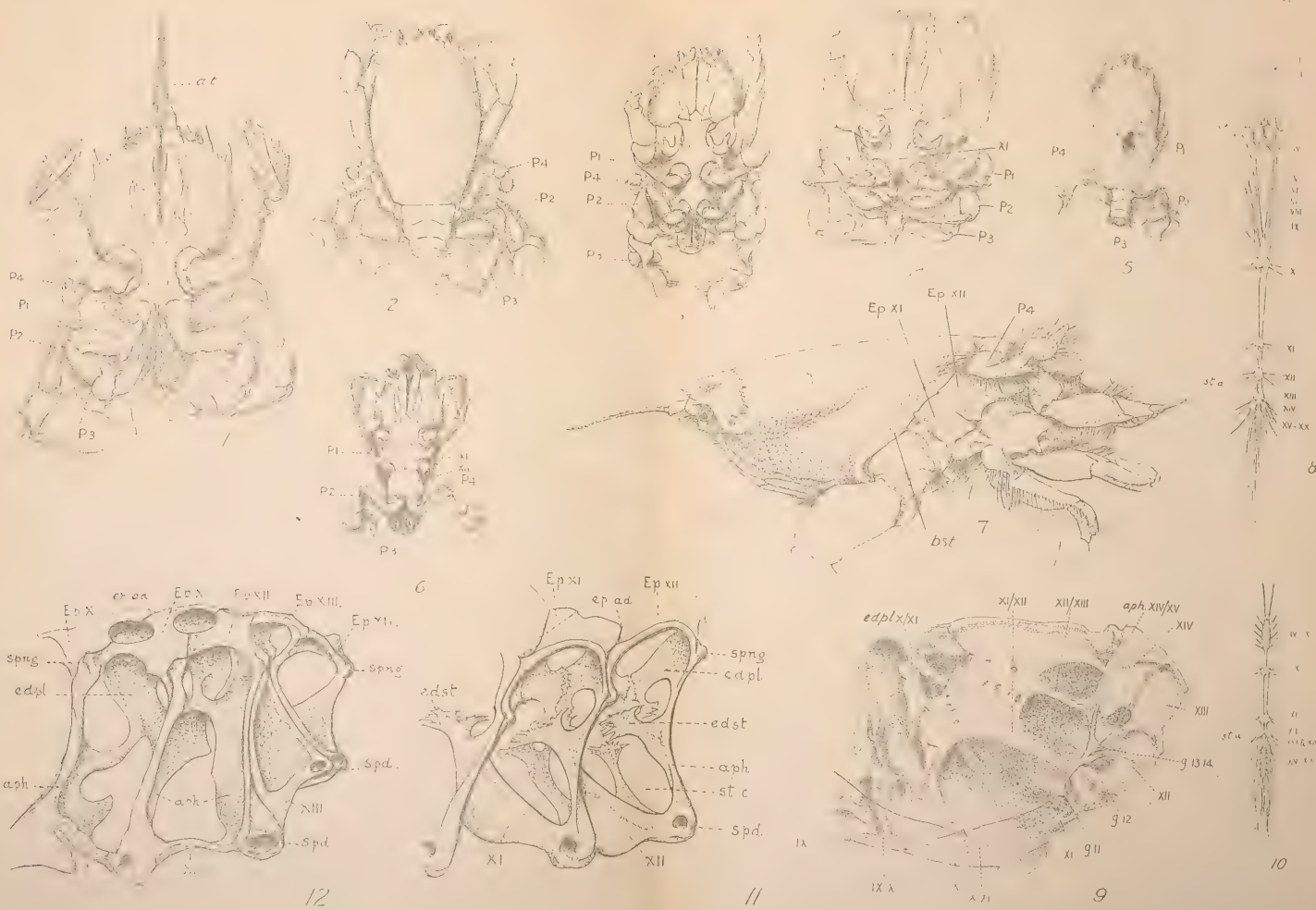
## PLATE 5.

- Fig. 13. A posterior view of the thoracic skeleton of the common lobster, showing the large size of the penultimate and the structure of the last thoracic sternum.
- Fig. 14. A posterior view of the thoracic skeleton of *Ranina dentata*, illustrating the shape of the last three thoracic sterna and the formation of the sella turcica posterior. *sg.a.* sagittal apodemes.
- Fig. 15. A similar view of the thoracic skeleton of *Dromia vulgaris*. In the absence of sagittal apodemes in the posterior thoracic sterna the arthrophragms xiv/xv do not meet in the middle line, and there is no sella turcica.
- Fig. 16. The endophragmal skeleton of *Notopus dorsipes* as seen from above after removal of the upper parts of the epimera. 6, 7, 8, the articular cavities of the second maxilla and first and second maxillipeds. The endosternites *edst.* and endopleurites *edpl.* are clearly shown.

- Fig. 17. Thoracic skeleton of *Notopus dorsipes* seen from the left side, illustrating the great depth of the epimera and the oblique raised ridge on the 11th, 12th, and 13th epimera, against which the lower margin of the branchiostegite fits: ix, x, the ninth and tenth sterna; vi/vii to ix/x. intersegmental arthropodagms.
- Fig. 18. Frontal view of the thoracic skeleton of *Notopus dorsipes*. The articular socket of the second maxilla of the left side is omitted.
- Fig. 19. The antennary region of *Nephrops norvegicus*. The rostrum is cut short and the eyes, antennules, and antennæ are removed from their sockets. i. The membranous ocular sternum; ii. the antennular sternum; iii. the antennary sternum; iv. the mandibular sternum; ii/iii. the arthropodagm between the antennular and antennary fossæ. x. sclerite identified as the mandibular epimeron.
- Fig. 20. Side view of the ocular and the antennary regions of *Nephrops norvegicus*. The rostrum is cut short and the antennules and antennæ are removed. *oct.* sclerite representing the tergum of the ocular segment; i. the sternum of the ocular segment: the epimera of this segment are membranous.
- Fig. 21. Antennary region and buccal frame of *Æthusina gracilipes*, Miers. *Ep.* iv. epimeron of the mandibular segment.
- Fig. 22. Antennary region and buccal frame of *Notopus dorsipes*. The appendages have been removed, with the exception of the right ocular peduncle and the left mandible. *A*<sub>1</sub>, *A*<sub>2</sub>, sockets of the antennules and antennæ; *pgt.* sub-antennary lobe of the pterygostome.
- Fig. 23. A similar view of the antennary region and buccal frame of *Ranina dentata*.

## PLATE 6.

- Fig. 24. A similar view of the antennary region and buccal frame of *Notosceles chimmonis*.
- Fig. 25. A similar view of the antennary region and buccal frame of *Lyreidus tridentatus*, showing the great elongation of the antennary sternum iii. *pgl.* paraglossæ.
- Fig. 26. Perspective sketch of the buccal frame of *Ranina dentata*, to show the hood-shaped mandibular sternum iv.
- Fig. 27. Antennary region and buccal frame of *Dromia vulgaris*. The appendages have been removed, with the exception of the right ocular peduncle.
- Figs. 28-33. *Notopus dorsipes*. Fig. 28. Right antennule: admedian aspect.
- Figs. 29 & 29 a. Right antenna, admedian and outer aspects. 1-5, segments of the peduncle.
- Fig. 30. Second maxilla with scaphognathite.
- Fig. 31. First maxilliped. Fig. 32. Second maxilliped: note the relatively large flagellum of the exopodite. Fig. 33. Third maxilliped: note the oblique line of hairs on the ischium also seen in *Ranilia*, M. Edw.
- Fig. 34, outer and Fig. 34 a, admedian views of the right antennule of *Ranina dentata*. Note the external opening of the statocyst, *scy*.
- Fig. 35, outer and Fig. 35 a, admedian views of the right antenna of *Ranina dentata*. 1-5, segments of peduncle.
- Fig. 36. Outer aspect of the right antennule of *Raninoides personatus*. Note the infolding of the cuticle to form the statocyst, and the external aperture of the latter at *scy*.
- Fig. 37. Admedian view of the right antenna of *Raninoides personatus*. In this genus and in *Lyreidus* the two basal segments of the peduncle are indistinguishably fused together.
- Fig. 38. Admedian view of right antennule of *Lyreidus tridentatus*.
- Fig. 39. Admedian view of right antenna of *Lyreidus tridentatus*.
- Fig. 40. Admedian view of right antennule of *Notosceles chimmonis*.
- Fig. 41, outer and Fig. 41 a, admedian views of the right antenna of *Notosceles chimmonis*.
- Fig. 43. *Notosceles chimmonis*. Third maxilliped.



G. C. Davis. 11.

Grand. Sc. 5 emb.

RANINIDÆ.

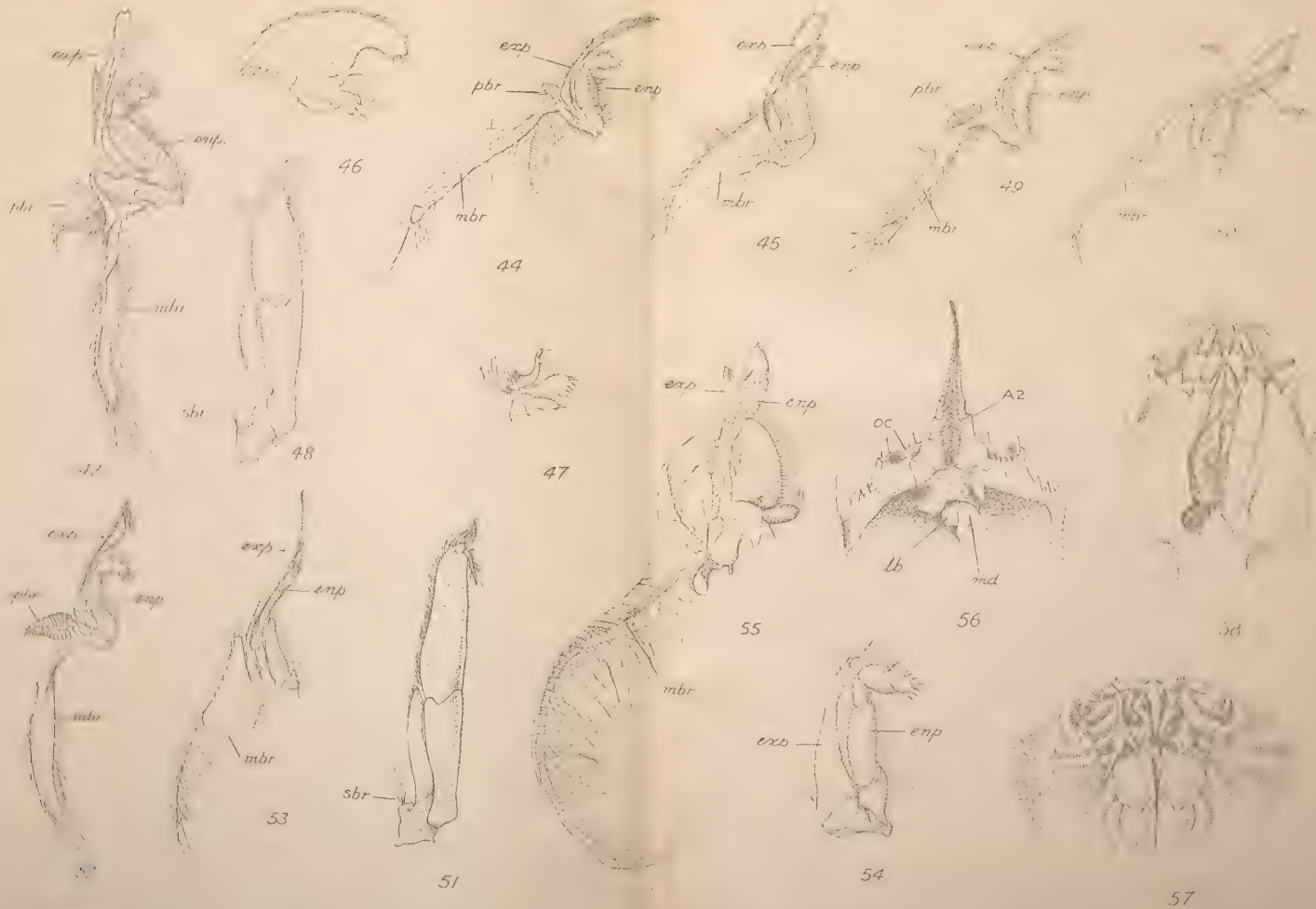


RANINIDÆ.





HAMINIDÆ



RANINIDÆ.

## PLATE 7.

- Fig. 42. Right second maxilliped of *Ranina dentata*. The exopodite is deeply grooved on its surface and has no flagellum.
- Figs. 44-47. *Notosceles chimmonis*. Fig. 44. Second maxilliped, the exopodite of which, like that of *Ranina*, is deeply grooved on the ventral surface and bears no flagellum. Fig. 45. First maxilliped. Fig. 46. Second maxilla with scaphognathite. Fig. 47. First maxilliped.
- Figs. 48-50. *Raninoides personatus*. Fig. 48. Third maxilliped. Fig. 49. Second maxilliped, the exopodite of which bears a minute flagellum. Fig. 50. First maxilliped.
- Figs. 51-53. *Lyreidus tridentatus*. Fig. 51. Third maxilliped. Fig. 52. Second maxilliped, the exopodite of which bears a minute flagellum. Fig. 53. First maxilliped, the exopodite of which is elongated in correlation to the elongation of the antennary sternum.
- Fig. 54. Second maxilliped of *Philyra levis*. The podobranch and mastigobranch are wanting; the exopodite is not grooved on the ventral surface and bears a short flagellum.
- Fig. 55. First maxilliped of *Philyra levis*. The mastigobranch is of great length and the exopodite is of normal shape and bears a flagellum. These appendages of *Philyra* should be compared with the corresponding appendages of the several genera of *Raninidæ*.
- Fig. 56. *Notopus dorsipes*: ventral view of the antennary region to show the relation of the respiratory tube to the antennary sternum. The pterygostomial portions of the carapace have been cut away.
- Fig. 57. Frontal view of *Notosceles chimmonis* to show the antennæ in their natural position and their relation to the orbits. The right antenna has been pulled slightly outwards to expose the antennules.
- Fig. 58. Ventral view of the anterior part of thorax and head of *Raninoides personatus*. The right third maxilliped has been removed and the left displaced from the middle line to expose the mouth frame and to show the elongated exopodites and endopodites of the first maxillipeds forming the floor of the spout-shaped antennary sternum. The latter extends well forward between the basal joints of the antennules.